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EBERLING, ALFRED W., and RICHARD N. BRAY. Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California 703

KROUSE, JAY S. Incidence of cull lobsters, *Homarus americanus*, in commercial and research catches off the Maine coast 719

COLLINS, JEFF, and RICHARD D. TENNEY. Fishery waste effluents: A method to determine relationships between chemical oxygen demand and residue 725

BRINTON, EDWARD. Population biology of *Euphausia pacifica* off southern California 733

BISSON, PETER A., and GERALD E. DAVIS. Production of juvenile chinook salmon, *Oncorhynchus tshawytscha*, in a heated model stream 763

MANOOCH, CHARLES S., III. Reproductive cycle, fecundity, and sex ratios of the red porgy, *Pagrus pagrus* (Pisces: Sparidae) in North Carolina 775

HALL, ALICE S., FUAD M. TEENY, LAURA G. LEWIS, WILLIAM H. HARDMAN, and ERICH J. GAUGLITZ, JR. Mercury in fish and shellfish of the northeast Pacific. I. Pacific halibut, *Hippoglossus stenolepis* 783

HALL, ALICE S., FUAD M. TEENY, and ERICH J. GAUGLITZ, JR. Mercury in fish and shellfish of the northeast Pacific. II. Sablefish, *Anoplopoma fimbria* 791

WALTERS, JOHN F. Ecology of Hawaiian sergestid shrimps (Penaeidea: Sergestidae) 799

LORD, GARY E. Decision theory applied to the simulated data acquisition and management of a salmon fishery 837

HUNTER, JOHN R., and CAROL SANCHEZ. Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax* 847

WIDERSTEN, BERNT. Ceriantharia, Zoanthidea, Corallimorpharia, and Actiniaria from the continental shelf and slope off the eastern coast of the United States 857

ALVAREZ, JOSE, CHRIS O. ANDREW, and FRED J. PROCHASKA. Dual structural equilibrium in the Florida shrimp processing industry 879

BLACKBURN, MAURICE, and WALTER NELLEN. Distribution and ecology of pelagic fishes studied from eggs and larvae in an upwelling area off Spanish Sahara 885

CRONE, RICHARD A., and CARL E. BOND. Life history of coho salmon, *Oncorhynchus kisutch*, in Sashin Creek, southeastern Alaska 897

YOUNGBLUTH, MARSH J. Vertical distribution and diel migration of euphausiids in the central region of the California Current 925

(Continued on back cover)

Seattle, Washington

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Fishery Bulletin

CONTENTS

Vol. 74, No. 4 October 1976

EBERLING, ALFRED W., and RICHARD N. BRAY. Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California 703
KROUSE, JAY S. Incidence of cull lobsters, *Homarus americanus*, in commercial and research catches off the Maine coast 719
COLLINS, JEFF, and RICHARD D. TENNEY. Fishery waste effluents: A method to determine relationships between chemical oxygen demand and residue. 725
BRINTON, EDWARD. Population biology of *Euphausia pacifica* off southern California 733
BISSON, PETER A., and GERALD E. DAVIS. Production of juvenile chinook salmon, *Oncorhynchus tshawytscha*, in a heated model stream 763
MANOOCH, CHARLES S., III. Reproductive cycle, fecundity, and sex ratios of the red porgy, *Pagrus pagrus* (Pisces: Sparidae) in North Carolina 775
HALL, ALICE S., FUAD M. TEENY, LAURA G. LEWIS, WILLIAM H. HARDMAN, and ERICH J. GAUGLITZ, JR. Mercury in fish and shellfish of the northeast Pacific. I. Pacific halibut, *Hippoglossus stenolepis* 783
HALL, ALICE S., FUAD M. TEENY, and ERICH J. GAUGLITZ, JR. Mercury in fish and shellfish of the northeast Pacific. II. Sablefish, *Anoplopoma fimbria* 791
WALTERS, JOHN F. Ecology of Hawaiian sergestid shrimps (Penaeidea: Sergestidae) 799
LORD, GARY E. Decision theory applied to the simulated data acquisition and management of a salmon fishery 837
HUNTER, JOHN R., and CAROL SANCHEZ. Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax* 847
WIDERSTEN, BERNT. Ceriantharia, Zoanthidea, Corallimorpharia, and Actiniaria from the continental shelf and slope off the eastern coast of the United States. ... 857
ALVAREZ, JOSE, CHRIS O. ANDREW, and FRED J. PROCHASKA. Dual structural equilibrium in the Florida shrimp processing industry 879
BLACKBURN, MAURICE, and WALTER NELLEN. Distribution and ecology of pelagic fishes studied from eggs and larvae in an upwelling area off Spanish Sahara 885
CRONE, RICHARD A., and CARL E. BOND. Life history of coho salmon, *Oncorhynchus kisutch*, in Sashin Creek, southeastern Alaska 897
YOUNGBLUTH, MARSH J. Vertical distribution and diel migration of euphausiids in the central region of the California Current 925

(Continued on next page)

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SCHERBA, STEPHEN, JR., and VINCENT F. GALLUCCI. The application of systematic sampling to a study of infauna variation in a soft substrate environment 937
KROUSE, JAY S. Size composition and growth of young rock crab, *Cancer irroratus*, on a rocky beach in Maine 949
DOTSON, RONALD C. Minimum swimming speed of albacore, *Thunnus alalunga*.. 955
BAILEY, JACK E., JEROME J. PELLA, and SIDNEY G. TAYLOR. Production of fry and adults of the 1972 brood of pink salmon, *Oncorhynchus gorbuscha*, from gravel incubators and natural spawaning at Auke Creek, Alaska 961
KEENE, DONALD F., and WILLIAM G. PEARCY. Comparison of the most successful and least successful west coast albacore troll fishermen..... 973

Notes

GOLDBERG, STEPHEN R. Seasonal spawning cycles of the sciaenid fishes *Genyonemus lineatus* and *Seriphus politus*..... 983
KRAVITZ, MICHAEL J., WILLIAM G. PEARCY, and M. P. GUIN. Food of five species of cooccurring flatfishes on Oregon's continental shelf 984
RALSTON, STEPHEN. Age determination of a tropical reef butterflyfish utilizing daily growth rings of otoliths 990
ROTHLISBERG, PETER C., and WILLIAM G. PEARCY. An epibenthic sampler used to study the ontogeny of vertical migration of *Pandalus jordani* (Decapoda, Caridea) 994
CARR, WILLIAM E. S., and THOMAS B. CHANEY. Harness for attachment of an ultrasonic transmitter to the red drum, *Sciaenops ocellata*..... 998

INDEX, VOLUME 74..... 1001

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DAY VERSUS NIGHT ACTIVITY OF REEF FISHES IN A KELP FOREST OFF SANTA BARBARA, CALIFORNIA

ALFRED W. EBELING AND RICHARD N. BRAY[1]

ABSTRACT

Vertical distributions and feeding activities of residential kelp-bed fishes were compared between day and night in an area of reef and kelp off Santa Barbara, Calif. Abundances and positions of fishes within four vertically oriented zones were observed during 42 paired day and night scuba transects made throughout the year along a line secured to a high-relief rocky reef located about 1.6 km offshore. Feeding activity was determined for surfperches (Embiotocidae) from the proportion of fish collected during the day or night having empty "foreguts," and inferred for other fishes from general observations of individuals. Although almost all of the 25 common fish species recorded were seen both day and night, the number seen and the degree of activity of most of these species decreased considerably at night. Many fishes that fed and moved about in mid-water well above the reef during the day were found in holes and crevices in the reef at night; others that foraged on or just above the bottom during the day showed little change in their position; and still others tended to disperse to adjacent areas of the reef. Daytime aggregations of fishes centered around the crest of the reef and other productive prominences and invariably dispersed at night. Unlike tropical communities of reef fishes, the kelp-bed community included neither a broad replacement for diurnal planktivores in the night shift nor a contingent that moves out over nearby sand flats to forage at night. Kelp-bed fishes showed considerable intraspecific variability in behavior. Thus, the kelp-bed community appears to be more loosely "programmed" even though it follows the same basic pattern of diel activity as the tropical-reef community. The kelp-bed species that belong to primarily tropical families tended to be quite specialized in their nocturnal sheltering behavior. Yet the primarily temperate surfperches, for example, simply became somewhat lethargic and remained exposed at night.

Day-night variations in the activities of reef fishes have received considerable attention recently, especially as these variations may relate to foraging methods (Hobson 1975), and to sharing of limited space (Smith and Tyler 1972). Direct observations of coral reef fishes have shown that, although most species are active mainly during the day, a substantial number are active only during the night (Hobson 1965, 1968, 1974; Starck and Schroeder 1965; Smith and Tyler 1972). In both instances, fish forage mainly during their active periods and school and/or seek shelter during their inactive periods (Hobson 1972). Dawn and dusk are important transitional periods when fishes that had been active seek shelter, when fishes that had been resting begin foraging, and when piscivores become most effective (Hobson 1972; Collette and Talbot 1972; Domm and Domm 1973).

The assemblage of fishes at a particular place on a tropical reef at night may differ markedly from the assemblage gathering at the same place during the day because foraging and sheltering activities do not always occur in the same area. For example, some surgeonfishes (Acanthuridae) and damselfishes (Pomacentridae), which shelter at night in the shallower portions of coral reefs, migrate offshore at dawn to their feeding grounds in deeper water (Hobson 1972). Nocturnal predators may undergo even more extensive migrations. Some snappers (Lutjanidae) and grunts (Pomadasyidae) are among a considerable number of species that move away from the reef at night to forage over surrounding sand flats (Hobson 1968, 1972). For many planktivores, however, the change in activity simply involves vertical movements from foraging areas in the water column to underlying sheltering sites (Hobson 1973). Thus the important events during the transition period between day and night include vertical as well as horizontal movements of fish.

Less is known about the nocturnal activities of temperate kelp-bed fishes. Some information has been available on a few species: the garibaldi, *Hypsypops rubicundus* (By Clarke 1970); the California sheephead, *Pimelometopon pulchrum* (by Wiley 1974); the kelp perch, *Brachyistius frenatus*; white seaperch, *Phanerodon furcatus*,

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and señorita, *Oxyjulis californica* (by Bray and Ebeling 1975); and the horn shark, *Heterodontus francisci*, and swell shark, *Cephaloscyllium ventriosum* (by Nelson and Johnson 1970). More recently, Hobson and Chess (1976) presented more comprehensive comparisons of the day and night feeding activities of fish off Santa Catalina Island: in particular, of the blacksmith, *Chromis punctipinnis*; the walleye surfperch, *Hyperprosopon argenteum*; the kelp rockfish, *Sebastes atrovirens*; the olive rockfish, *S. serranoides*; the queenfish, *Seriphus politus*; and the salema, *Xenistius californiensis*, as well as some of the others mentioned above. Therefore, we initiated a comparative day and night survey of the fishes inhabiting an area of reef and kelp off Santa Barbara, Calif., to see if the fish community undergoes a substantial diel change in its composition, vertical distribution, and activity.

METHODS

Naples Reef is a large rocky outcrop located 24 km west of Santa Barbara (lat. 34°25′N, long. 119°57′W). The reef measures 275 m by 80 m (2.2 hectares) and lies 1.6 km offshore. The substratum consists of a series of sandstone rills and ridges that run parallel to the coast. Depths across the reef average 8 to 10 m, although some prominences project to within 5 m of the surface. The bottom surrounding the reef is 16 to 20 m deep and is comprised of sand with rocky outcrops inshore, or sand and cobbles offshore. The assemblage of plant and animal life on and about the reef is among the richest along the Santa Barbara coast. Giant kelp (*Macrocystis*) is always present on the reef, although kelp densities fluctuated throughout the study period. Temperatures along the top of the reef ranged from 11°C in the spring to 19°C in the fall. Underwater visibility averaged 5 m at the transect line.

A transect line consisting of two 40-m segments was staked along either side, shoreward and seaward, of a high-relief ridge with a crest at 6 m. Day and night counts of fishes along the line were made by scuba divers. For each day-night pair of samples, we counted fish within 2 m on either side of the line. To minimize the effect of nondiel fluctuations on our observations, we always made the night transect member of a pair within 12 h of the day transect. A special effort was made to insure that the night counts of fish were made throughout approximately the same reef area and overlying volume of water as were the day counts. Powerful 10-cell underwater hand lights, fitted with reflectors to illuminate the data sheets, were used intermittently during the day to inspect holes, and used continuously throughout the night dives.

We evaluated the diel activities of fish species by observing the fishes' vertical distribution and feeding habits. During the transects, fish sightings were tallied in separate columns on our plastic data sheets according to the zone in which each individual was observed (Table 1).

The use of dive lights at night may have attracted or repelled fish depending on the species and/or altered their state of activity. Yet fishes normally inactive at night did not seem to be affected by brief exposures to dive lights. Species normally active at night responded in various ways, from showing hyperactivity to apparent immobilization. Other nighttime observations of reef fishes off California (Nelson and Johnson 1970) and in tropical waters (Hobson 1965; Starck and Davis 1966; Smith and Tyler 1972) also indicate that night-active fishes often respond unpredictably to artificial illumination.

Day and night differences in the feeding habits of many species were inferred either from direct observations of foragers or from changes in the fishes' vertical distribution and activity level (i.e., whether the fish were exposed and responsive to our presence or sheltered and unresponsive). We feel that such observations of fish activity by themselves were sufficient to distinguish feeding from nonfeeding periods for many of the more prominent species. However, such observations proved to be inadequate indicators of foraging activity for surfperches (Embiotocidae), which comprise the most abundant and diverse foraging guild of the fishes on Naples Reef. To test for diel differences in feeding activity of surfperches, therefore, we speared during all hours of day and night approximately 400 adults of the five common demersal species: the black perch, *Embiotoca jacksoni* (median standard length 195 mm, range

TABLE 1.—Zones of vertical orientation in which fish were observed along a transect line

Zone	Extent of zone
IV Mid-water	Greater than 1.0 m above the bottom, in open water and/or near kelp stipes
III Suprabenthic	Within 1.0 m of the bottom
II Bottom	In physical contact with the bottom yet exposed
I Shelter	In holes, crevices, or under ledges

86-244 mm); striped seaperch, *E. lateralis* (200, 110-280); rubberlip seaperch, *Rhacochilus toxotes* (279, 165-400); pile perch, *Damalichthys vacca* (210, 97-260); and rainbow seaperch, *Hypsurus caryi* (159, 114-253). Immediately after each dive, individuals were either iced and later frozen, or slit ventrally and fixed in 10% Formalin.[2] The procedure for gut analysis followed the method of Bray and Ebeling (1975), except that the surfperch's gut, which is simple and tubular and lacks a well defined "stomach," was divided into quarters. Fullness of the "foregut," defined as the first quarter of the length of the entire gut, was scored subjectively from 1 (empty) to 5 (full), and plotted against time of collection. Since fish were sampled throughout the year, their times of collection were seasonally adjusted relative to actual times of sunrise and sunset as determined from solar tables.

RESULTS

We identified 25 species of fishes from 21 paired day-night transects made between April 1972 and September 1973. Most of the fishes seen along the transect line were adults. The only abundant juveniles were of the blue rockfish, *Sebastes mystinus*. Hence for blue rockfish only, juveniles and adults were counted separately. We excluded from the analysis all species that could not be consistently observed, such as some of the more cryptic and secretive fishes that blend with their surroundings and hide in kelp and rocks, and species that occur only near the water surface outside our field of vision.

It appeared that our visual counts adequately sampled all of the more conspicuous kelp-bed fishes. The rank order of abundance of fishes recorded in the 21 daytime transects was highly correlated with that of fishes observed in a photographic survey consisting of 125, 2.5-min motion pictures (Ebeling, Larson, and Alevizon unpubl. data) filmed over the same area (Kendall's tau coefficient of rank correlation = 0.65; $P < 0.001$).

The species composition of seasonally pooled samples and the relative abundances of the different species varied surprisingly little during the 17-mo study period. Almost all species were seen throughout the year, and rank orders of species abundances, pooled over day and night samples, were significantly concordant among seasonal periods that correspond roughly to annual oceanographic periods defined by Brown (1974) (Table 2).

During the day, almost 4,000 fishes representing 11 families of teleosts and 1 family of sharks were counted along the transect line. The two dominant groups—surfperches (Embiotocidae) and rockfishes (*Sebastes*)—were represented by six species each. The most abundant species was *S. mystinus* whose juveniles accounted for 44% of the individuals sighted during the day (Table 3).

Most individuals of all species of fishes (66%) were observed in the mid-water zone higher than 1 m off the bottom (Table 4). The two most abundant species in the mid-water zone, *S. mystinus* and *Chromis punctipinnis* often formed large, mixed aggregations above rocky prominences and around columns of giant kelp. Besides *S. mystinus* and *C. punctipinnis*, more than 80% of the individuals in several other species were observed in the mid-water zone: the kelp bass, *Paralabrax clathratus*; *Oxyjulis californica*; opaleye, *Girella nigricans*; and *S. serranoides* (Table 4). But 10 of the total of 19 species recorded from the mid-water zone were more abundant in other zones.

Some 25% of the total individuals of all species were observed in the suprabenthic zone, within 1 m of the rocky bottom (Table 4). This zone included the most species (21) and was dominated by surfperches: 71% of the individuals observed in the suprabenthic zone were surfperches, as compared with but 12% in the mid-water zone. Nearly half the individuals were *Embiotoca jacksoni* or *E. lateralis*.

Less than 10% of the total individuals recorded during the day were observed either in the bottom zone, contacting the reef in an exposed position, or in the shelter zone, occupying a crevice or hole (Table 4). Most of these were demersal, "ambusher-type" predators, e.g., rockfishes and sculpins (Cottidae), although a few of the mid-water species, e.g., *S. mystinus* and *C. punctipinnis*, were also observed in these zones in small numbers.

We recorded substantially fewer individuals at night than during the day (Table 3). Day to night decreases in total numbers were consistently significant among the 21 pairs of day-night samples (Wilcoxon signed-ranks test for paired observations, $P < 0.005$). Also, lists of species, ranked by abundance, differed at night. All 21 rank correlations for the day-night sample pairs (tau = -0.32 to +0.22), as well as the single rank correla-

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.–Seasonal variation in relative abundance of fishes observed along a transect line. Samples are pooled over day and night transects by trimonthly intervals generally coinciding with periods of oceanographic change off Santa Barbara. Kendall's *W* coefficient of rank concordance among seasons = 0.77 ($P<<0.005$).

Species	Percent of total individuals by season			
	Dec.-Feb.	Mar.-May	June-Aug.	Sept.-Nov.
Sebastes mystinus (juvenile)	29.5	29.4	45.3	25.2
Chromis punctipinnis	21.3	11.1	14.5	14.9
Embiotoca jacksoni	14.5	10.9	8.75	14.5
Oxylebius pictus	5.61	3.97	2.05	3.71
Embiotoca lateralis	4.97	2.34	1.49	1.86
S. carnatus	3.71	4.69	2.33	3.12
Hyperprosopon argenteum	3.29	2.71	1.40	8.27
S. mystinus (adult)	2.09	6.40	1.77	9.20
Pimelometopon pulchrum	1.95	0.36	0.84	0.42
Damalichthys vacca	1.86	3.07	2.98	2.36
Rhacochilus toxotes	1.44	1.89	0.47	1.27
Hypsypops rubicundus	1.30	1.17	1.86	1.94
Coryphopterus nicholsii	1.25	0.18	0	0.84
Paralabrax clathratus	1.21	0.36	1.30	1.86
S. chrysomelas	1.21	0.81	0.65	1.10
Medialuna californiensis	0.97	0.09	0.28	0.17
Scorpaenichthys marmoratus	0.84	0.27	0.09	0.08
Hypsurus caryi	0.56	13.6	3.17	1.86
Oxyjulis californica	0.56	2.34	1.12	2.62
Phanerodon furcatus	0.51	2.89	4.28	0.17
Ophiodon elongatus	0.46	0.18	0.09	0
Girella nigricans	0.37	0.27	2.70	3.04
Sebastes serriceps	0.19	0.36	0.37	0
S. serranoides	0.14	0.09	1.77	0.76
Cephaloscyllium ventriosum	0.19	0.09	0	0.34
S. atrovirens	0.05	0.45	0.37	0.34
Total no. of individuals	2,150	1,109	1,074	1,185
Total no. of transects	14	10	10	8

TABLE 3.–Day-night variation in abundance of fishes observed along a transect line. Samples are pooled over seasonal intervals (see Table 2). Symbols in the "Difference" column indicate for each species whether the numbers of individuals observed during the day, ordered among all transects, were significantly greater than (>), less than (<), not significantly different from (=), or too few to compare with (NC) the numbers observed at night (Wilcoxon signed-rank test for paired observations, $P\leq0.05$).

Species	No. of individuals		Percent of total individuals		Difference day vs. night
	Day	Night	Day	Night	
Sebastes mystinus (juvenile)	1,730	8	43.80	0.51	>
Embiotoca jacksoni	492	207	12.40	13.20	>
Chromis punctipinnis	253	662	6.40	42.30	<
Oxylebius pictus	215	16	5.44	1.02	>
S. mystinus (adult)	210	34	5.31	2.17	>
Hypsurus caryi	188	31	4.75	1.98	=
Embiotoca lateralis	134	37	3.39	2.37	>
Damalichthys vacca	112	22	2.83	1.41	>
Phanerodon furcatus	91	0	2.30	0	>
Oxyjulis californica	81	0	2.05	0	>
Girella nigricans	70	6	1.77	0.38	>
Paralabrax clathratus	65	2	1.64	0.13	>
S. carnatus	56	138	1.42	8.82	<
Hypsypops rubicundus	55	29	1.39	1.85	>
Pimelometopon pulchrum	41	19	1.04	1.21	=
Coryphopterus nicholsii	38	1	0.96	0.06	>
Rhacochilus toxotes	31	41	0.78	2.62	=
S. serranoides	21	11	0.53	0.70	=
Medialuna californiensis	19	8	0.48	0.51	=
S. chrysomelas	17	38	0.43	2.43	<
Scorpaenichthys marmoratus	12	11	0.30	0.70	=
Ophiodon elongatus	10	3	0.25	0.19	=
Sebastes atrovirens	7	7	0.18	0.45	NC
S. serriceps	4	8	0.10	0.51	=
Cephaloscyllium ventriosum	2	11	0.05	0.70	NC
Hyperprosopon argenteum	0	214	0	13.70	<
Total no. of individuals	3,954	1,564	100.0	100.0	
Total no. of transects	21	21	21	21	

TABLE 4.—Vertical-zone variation in numbers of fishes observed along a transect line compared between day and night. Vertical zones are defined in Table 1; the Δh measure of a species' change in vertical position between day and night is defined in the text.

	Day				Night				
Family and species	Mid-water	Supra-benthic	Bottom	Shelter	Mid-water	Supra-benthic	Bottom	Shelter	Δh
Scyliorhinidae:									
Cephaloscyllium ventriosum	0	1	0	1	0	1	6	4	0.27
Serranidae:									
Paralabrax clathratus	54	11	0	0	1	0	0	1	1.33
Kyphosid-like fishes:									
Girella nigricans	65	5	0	0	0	2	4	0	1.60
Medialuna californiensis	6	13	0	0	0	3	4	1	1.07
Embiotocidae:									
Damalichthys vacca	32	76	2	2	10	10	2	0	−0.13
Embiotoca jacksoni	101	386	4	1	66	84	51	6	0.18
E. lateralis	26	108	0	0	10	15	10	2	0.30
Hyperprosopon argenteum	0	0	0	0	213	1	0	0	—
Hypsurus caryi	97	90	1	0	7	6	16	2	0.93
Phanerodon furcatus	64	27	0	0	0	0	0	0	—
Rhacochilus toxotes	8	19	4	0	16	20	4	1	−0.12
Pomacentridae:									
Chromis punctipinnis	210	30	0	13	5	9	38	610	2.62
Hypsypops rubicundus	8	32	5	10	0	0	1	28	1.66
Labridae:									
Oxyjulis californica	73	8	0	0	0	0	0	0	[1]2.91
Pimelometopon pulchrum	29	10	0	2	0	0	0	19	2.61
Gobiidae:									
Coryphopterus nicholsii	0	0	32	6	0	0	1	0	−0.16
Scorpaenidae:									
Sebastes atrovirens	2	3	1	1	2	2	2	1	0.14
S. carnatus	3	6	32	15	0	10	84	44	0.19
S. chrysomelas	0	0	10	7	0	0	19	19	0.09
S. mystinus (adult)	178	21	10	1	4	2	8	20	2.08
S. mystinus (juvenile)	1,606	119	0	5	0	1	1	6	2.55
S. serranoides	18	3	0	0	9	0	0	2	0.40
S. serriceps	0	0	1	3	0	0	2	6	0
Hexagrammidae:									
Ophiodon elongatus	2	4	4	0	0	0	0	3	1.80
Oxylebius pictus	4	24	179	8	0	0	6	10	0.74
Cottidae:									
Scorpaenichthys marmoratus	0	1	10	1	0	0	10	1	0.09
Total no. of individuals	2,586	997	295	76	343	166	269	786	
Percent of day or night total	65.4	25.2	7.46	1.92	21.9	10.6	17.2	50.3	
Total no. of transects	21	21	21	21	21	21	21	21	

[1]Individuals are assumed to bury themselves at night.

tion for the day-night contrast with samples pooled (tau = 0.13), were nonsignificant ($P>0.05$). A Wilcoxon signed-ranks test for paired (day-night) observations indicated that numbers of eight species did not differ significantly between day and night, while numbers of four species actually increased (Table 3).

Two species commonly observed during the day were either seldom or not seen at night: *Phanerodon furcatus* and *Oxyjulis californica*. Although we often saw individuals of *P. furcatus* browsing on bryozoan-encrusted algae (mainly *Gelidium* sp.) along a crest of the reef during the day, we rarely observed them at night along the crest and never observed them during regular transects. We commonly saw small groups of *O. californica* in the mid-water zone above the transect lines during the day. At dusk, however, *Oxyjulis* individuals bury themselves in rubble and sand on the reef and remain covered until dawn (Herald 1961; Feder et al. 1974; Bray and Ebeling 1975).

Only one species was seen at night but never during the day. *Hyperprosopon argenteum* was the second-most abundant species recorded at night, although it was never seen around the transect line during daylight hours. In over 6 yr of observations, we have seen this species in kelp beds on only a few occasions during the day. Schools of *H. argenteum* commonly occur in shallow waters along sandy beaches and shallow reefs during the day, so it appears that at least some of the larger individuals migrate offshore to kelp beds at dusk. To reach Naples Reef, fish near the surf would have to swim approximately 1.6 km offshore.

Resemblance between the day and night samples of $S = 25$ species within each of the four vertical zones was measured by coefficients of similarity or "overlap" (cf. Colwell and Futuyma

1971). Similarity (C) is scaled from 0 (no resemblance at all) to 1.0:

$$C = 1.0 - \tfrac{1}{2} \sum_{i=1}^{s} |P_{ij} - P_{ik}|,$$

where P_{ij} = the proportionate abundance of species i in day sample j, and P_{ik} = that in night sample k.

Though the mid-water zone abounded with fishes during the day, it appeared sparsely populated at night (Table 4). Day-night similarity within the mid-water zone was the least ($C = 0.12$) for the four zones. Six of the 10 species recorded from the mid-water zone at night were surfperches, while three of the remaining four were rockfishes. *Hyperprosopon argenteum* accounted for 62% of the total fish recorded in this zone. *Damalichthys vacca*, along with *Sebastes serranoides* and adult *S. mystinus*, were often seen scattered in the water column at night.

Although the suprabenthic zone underwent a substantial reduction in fish abundance at night, its day-night species similarity was the highest ($C = 0.67$) for the four zones. During both day and night, the suprabenthic zone was dominated by surfperches. At night, surfperches comprised the four most abundant species, accounting for almost 80% of the total fishes observed in the suprabenthic zone (Table 4). Although Pacific electric rays (*Torpedo californica*) were never recorded over the transect lines, they were often encountered nearby, swimming slowly and hovering above the bottom (Bray, Hixon, and Ebeling unpubl. data). Swell sharks (*Cephaloscyllium ventriosum*), whose nocturnal activities were investigated by Nelson and Johnson (1970), were occasionally seen swimming just above the reef at night.

Fish observed in the bottom zone increased from 7.4% of the total individuals recorded from all zones during the day to 17.1% of the total at night (Table 4). The zone's relatively low day-night species similarity ($C = 0.28$) was due to variations in numbers of the demersal ambusher-type predators and increases in numbers of "resting" surfperches. Among the ambusher-type species, e.g., numbers of painted greenling, *Oxylebius pictus*, decreased from 179 counted during the day to only 6 at night, and numbers of two common rockfishes increased: the black-and-yellow, *S. chrysomelas*, almost doubled and the gopher, *S. carnatus*, almost tripled (Table 4).

At night, most fishes were observed in the shelter zone. Although only 2% of the day total of fishes were seen in holes and crevices, 50% of the night total were observed there (Table 4). Day-night species similarity was fairly low ($C = 0.36$), largely because of the increase in numbers of individuals of *Chromis punctipinnis* observed in holes: from only 13 counted during the day to 610 counted at night (Table 4). Individuals of *Pimelometopon pulchrum* and *S. mystinus* were also commonly seen in the shelter zone at night.

These counts of fishes inhabiting holes, especially at night, may be conservative because we could not completely census the numerous deep holes and crevices along the transect line. This problem certainly influenced our counts of individuals of *O. pictus* and juvenile *S. mystinus*. Nocturnal counts of both species were much lower than those made during the day, and the individuals that were observed at night were invariably hiding deep in holes. Subsequent nighttime applications of small amounts of the anesthetic quinaldine to holes that first appeared vacant often yielded several *O. pictus* and 5 to 20 juvenile *S. mystinus*. Similar applications of this anesthetic during the daytime occasionally revealed these fishes, but in far smaller numbers.

The vertical positions of the 25 species of fishes during the day and night are summarized in Table 4. Data on some species are fragmentary because individuals of these species were rarely encountered along the transect line. However, general observations made during hundreds of hours of diving during both day and night tend to substantiate conclusions based on these data. For example, we saw but two kelp bass along the transect line at night, one in mid-water, the other on the bottom. In surrounding areas, we saw many individuals resting on the bottom, several in mid-water, but very few in holes. Eighteen of 24 species recorded during the day were most common in the suprabenthic and mid-water zones above the reef. Only the treefish, *S. serriceps*, was most common in the holes of the shelter zone. Of the 23 species recorded at night 16 were most common in contact with the reef, either in the open positions of the bottom zone or in the holes of the shelter zone. Only two species, *Hyperprosopon argenteum* and *S. serranoides*, were most common in the mid-water zone.

The day-night differences in the activities of many species involved considerable shifts among

the four zones. These shifts are measured in Table 4 by values of Δh:

$$\Delta h = \sum_{i=1}^{4} \left[(p_{i\,\mathrm{day}})(i) - (p_{i\,\mathrm{night}})(i) \right],$$

where $p_{i\,\mathrm{day}}$ is the proportion of individuals of a species observed during the day in zone i (i = 1,2, 3, or 4 for the shelter through mid-water zones, respectively) and $p_{i\ \mathrm{night}}$ is the proportion observed at night. The Δh's range from +3.0, when all observed individuals of a species undergo a maximum shift downward from the mid-water zone during the day to the shelter zone at night, to -3.0, when all individuals undergo the reverse maximum shift upward. A $\Delta h = 0.0$ indicates little or no shift, in that the species' proportional distribution among zones does not change from day to night.

Fish species varied considerably in the degree to which they changed zones between day and night, although the patterns of shifting upward or downward were similar within families (Table 4). Some species changed their vertical position little if at all: several species of rockfishes; the cabezon, *Scorpaenichthys marmoratus*; *Rhacochilus toxotes*; *Damalichthys vacca*; and blackeye goby, *Coryphopterus nicholsii*. Other species changed their vertical position markedly between day and night. Individuals of *Chromis punctipinnis* and *Pimelometopon pulchrum*, which had near-maximum positive values of Δh, move about in the water column during the day and shelter in holes at night. No individuals of *Oxyjulis californica* were seen at night (recall that they descend from mid-water to bury themselves in sand or gravel patches). Assuming that burying individuals are in the "shelter zone," Δh for *Oxyjulis* = 2.91. No species had a large negative value of Δh, i.e., no species mostly contained individuals that rose from the bottom to mid-water at night. Hobson and Chess (1976) noted that during the day most *Sebastes atrovirens* were "seated on rocky strata" whereas at night they "hovered in mid-water." In the present study, the Δh of *S. atrovirens* was small but positive (Table 4); however, this species was relatively rare in our transects.

Several lines of evidence indicate that many of the kelp-bed fishes observed become less active and do not regularly feed at night. The levels of activity often could be inferred from direct observations. Many species that swam about and fed on or above the reef during the day were found deep in holes and crevices at night and would flee from their shelter only when vigorously disturbed. These species included *Hypsypops rubicundus*, *C. punctipinnis*, *P. pulchrum*, and juvenile *S. mystinus*. Some individuals of *P. pulchrum* reportedly secrete a mucous envelope about themselves (Wiley 1974), and we often found this fish wedged deep in crevices in an apparent state of torpor at night. Individuals of *Girella nigricans* were also found in holes or on the bottom but were more responsive to our presence. Previous diel analyses of gut contents substantiate our present impressions that the following species are strictly daytime feeders: *H. rubicundus* (by Clarke 1970), *O. californica* (by Bray and Ebeling 1975), juvenile *S. mystinus* (by Thomas Bailey unpubl. data), and *C. punctipinnis* (by Hobson and Chess 1976; Bray unpubl. data).

Our analyses of fish-gut emptiness revealed that even many of the kelp-bed fishes not undergoing such obvious diel changes in vertical position may stop feeding at dusk (Figure 1, Table 5). Although all five demersal surfperches (*Embiotoca jacksoni*, *E. lateralis*, *Hypsurus caryi*, *Damalichthys vacca*, and *Rhacochilus toxotes*) generally remain in the suprabenthic and bottom zones both day and night, their diel patterns of gut emptiness indicate that all but *R. toxotes* do not feed at night. Median scores of gut fullness for *E. jacksoni* reached maximum values in the afternoon and declined after sunset; at dawn, all guts examined were empty (Figure 1a). Fully 88% of the fishes speared during daylight hours contained food in their foreguts (Table 5). Although 39% of the fishes collected at night contained food, 89% of these were collected before midnight. Thus it is likely that the food contained in the foreguts of these individuals was eaten before nightfall and had not yet passed into the second quarter of their guts. Foreguts of *E. lateralis*, *H. caryi*, and *D. vacca* show the same pattern (Figure 1b-d). In fact, all four species had significantly less food in their guts during the night than during the day (Table 5). Gnose (1968) also observed that individuals of *E. lateralis* collected from off Oregon had empty guts at dawn. Additionally, two other kelp-bed surfperches that commonly occur in mid-water, *Phanerodon furcatus* and *Brachyistius frenatus*, which is rare at Naples Reef, feed mainly during the day (Bray and Ebeling 1975; Hobson and Chess 1976).

In contrast, median scores for fullness of *R. toxotes* reached maximum values at night, and many foreguts were empty during the day (Figure

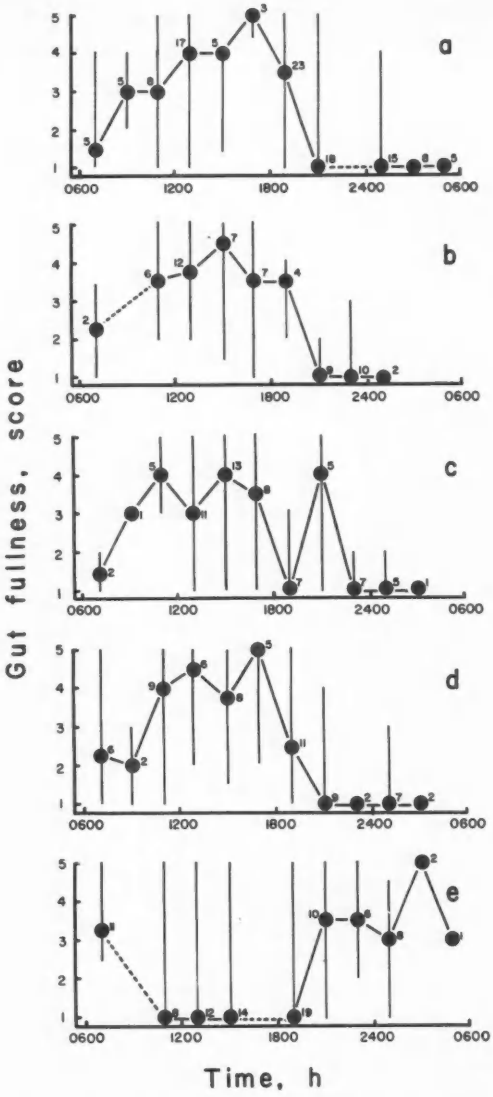

FIGURE 1.—Scored fullness (1, empty-5, full) of foreguts of five demersal surfperches: a, *Embiotoca jacksoni*; b, *E. lateralis*; c, *Hypsurus caryi*; d, *Damalichthys vacca*; and e, *Rhacochilus toxotes*. Each point represents the median score and each vertical line the range of scores for (n) individuals collected over a 2-h interval. Time is measured relative to sunrise (0600 h) and sunset (1800 h).

TABLE 5.—Day-night variation in "foregut" emptiness for the five species of demersal surfperches. Values of chi-square with 1 df were calculated from day-night, empty-not empty values in contingency tables for each species.

Species	Day		Night		Day vs. night	
	No. examined	% empty	No. examined	% empty	χ^2	P
Embiotoca jacksoni	43	12	69	61	26.4	<0.005
E. lateralis	34	5.9	25	64	23.0	<0.005
Hypsurus caryi	40	10	25	60	18.6	<0.005
Damalichthys vacca	36	8.3	31	71	27.9	<0.005
Rhacochilus toxotes	45	51	46	33	3.2	≈0.07

1e). Some 67% of the fish collected at night contained food in their foreguts, and 49% of those collected during the day also contained food, although this difference was not significant (Table 5).

It is likely that many of the large-mouthed demersal species feed any time that suitable prey are available. Included among these species are various rockfishes (*Sebastes carnatus*, *S. chrysomelas*, and *S. serriceps*) and *Scorpaenichthys marmoratus*, all of which are cryptically patterned and probably ambush much of their prey. Analyses of gut fullness and states of digestion relative to time of day may be of little value in determining the feeding chronology of these fishes, especially larger individuals. Kariya (1969) showed that food items may take days rather than hours to pass through the stomach of *Sebastes inermis*, a species from Japan; and Larson (pers. commun.) found that small majid crabs (10 mm carapace width) were still intact in the stomachs of adults of *S. carnatus* up to 10 h after ingestion. However, other lines of evidence indicate that they feed at night. We saw more individuals of *S. carnatus* and *S. chrysomelas* at night, probably because they were more active then, and the types of food items included in their diets suggest they feed at night as well as during the day. Their diets include medium-sized crustaceans (crabs, shrimps, etc.) and cephalopods (Quast 1968b; Larson 1972); both prey were far more active and exposed along the transect line at night. We have observed individuals of *S. carnatus* and *S. chrysomelas* at night with live, struggling crabs and octopi protruding from their mouths. Also, individuals of these species often consumed small fishes that escaped from our collecting spears during night dives. Finally, all of these fishes can be caught by hook and line at night as well as during the day (Milton Love, pers. commun.).

Along the transect line during the day, fishes congregate in mid-water to pick plankton and browse on kelp surfaces. At night, on the other hand, almost all of the foraging by fishes occurs on

or near the bottom. *Hyperprosopon argenteum* was an exception in that individuals of this species occurred alone or in small, loose groups in mid-water at night. Hobson and Chess (1976) and Bray (unpubl. data) found that guts of specimens speared at night were full of recently ingested prey, whereas almost all guts from individuals speared during the day were empty. However, the fact that this fish constitutes a large portion of the catch made by shore fishermen (Frey 1971) indicates that at least some individuals feed during the day.

We know little about the feeding periods of the remaining six species seen along the transect line. The halfmoon, *Medialuna californiensis*, often appeared to be more sensitive to our presence than were individuals of other species near the bottom, and we cannot deny the possibility that *Medialuna* feeds at night. It reportedly eats mainly algae supporting a variety of attached epiphytic animals and much smaller quantities of free animals (Quast 1968b; Follett et al. 1960). The fact that two small demersal species, *Coryphopterus nicholsii* and *Oxylebius pictus*, were seen much less often at night suggests that they retreat deep into holes and crevices then. Larger individuals of lingcod, *Ophiodon elongatus*; *Paralabrax clathratus*; and *S. mystinus* eat cephalopods as well as fishes and other prey (Love 1974; Miller and Geibel 1973; Quast 1968c), so it is reasonable to suspect that they too feed, at least occasionally, at night.

DISCUSSION

During the day, large numbers of fishes pervade the study area of reef and kelp off Santa Barbara. Most fishes inhabit the mid-water zone well off the bottom, while smaller numbers of ambusher-type predators remain in contact with the reef bottom. In contrast, the same kelp forest appears almost abandoned at night. Most notably, large numbers of fishes disappear from mid-water, while the numbers of fishes increase markedly in the shelter zone of holes and crevices.

Although day-night changes in fish abundance may be partly attributable to sampling error caused by our use of lights at night, etc., these changes most certainly reflect differences in the fishes' requirements and distributional patterns between their periods of activity and inactivity. During the day, the area in the vicinity of our transect line seems to constitute a focal point of fish activity. Daytime fish diversity and abundance appeared to be greater along the transect line than in adjacent areas, 5 to 10 m away. Loose aggregations of juvenile *S. mystinus* and, less frequently, *Chromis punctipinnis*, *P. clathratus*, and *Girella nigricans*, formed in the water column above the transect line. Likewise, other fishes gathered closer to the bottom. Perhaps this local richness relates to the position of the transect about the reef crest. The transect line was attached to one of the highest rocky prominences on the reef, and it ran along the inner margin of a dense stand of giant kelp. Quast (1968a) noted that the combination of high-relief rocks and kelp augments the surface area available for invertebrates, the principal food of the fishes, and serve as orientation points for fishes throughout the water column. Also, inshore and offshore margins of kelp beds often demonstrate the "edge-effect," in that the fauna is richer there than in areas on either side (Feder et al. 1974). At Naples Reef, surfperches, especially individuals of *Embiotoca lateralis* and *Phanerodon furcatus*, tend to congregate about the reef crest and the south dropoff 20 m away where thick stands of *Gelidium* and other red algae flourish. Individuals of *E. lateralis* gorge themselves on the caprellid amphipods that occur in great numbers amongst the algae (Robert Cowen and David Laur, pers. commun.). Also we noticed that fishes tend to aggregate in sunlit areas like the reef crest and avoid the shaded areas on either side. In tropical reefs, diurnally schooling fishes that migrate to adjacent sand flats at night return in daylight to the same prominent topographic features on the reef (Hobson 1973). Other factors that influence local fish abundance and diversity are: availability of food (e.g., Hobson 1968, 1972, 1974), proximity to shelter (e.g., Low 1971; Sale 1972), and the presence of "cleaner" fish that rid larger fish of their ectoparasites (Slobodkin and Fishelson 1974). At least some of these factors may also have contributed to the high numbers of fish along our transect line.

After dark, fishes that seek shelter and/or become inactive are no longer attracted by richer feeding grounds and orientation points characteristic of the reef crest. As darkness falls, mid-water aggregations of *C. punctipinnis*, *Paralabrax clathratus*, *Girella nigricans*, and young *S. mystinus* dissolve as the fish disperse singly or in small groups over the bottom to shelter in the many holes and crevices in surrounding areas. During the day, for example, individuals of *C.*

punctipinnis occur patchily in small mid-water aggregations over the transect line and in much larger aggregations along the outer margins of the kelp bed. At night, however, they shelter in holes throughout the entire study area. In freshwater lakes of Ontario at night, day-active fishes move into shallow water where there is sufficient cover for sheltering (Emery 1973), but in the tropics, most day-active reef fishes shelter in holes deep in the coral and so their exposed numbers decrease at night (see Hobson 1974).

The decrease in nocturnal abundance of fishes in the transect area might have been caused by their migrations to nearby areas of sand. Over coral reefs, many of the more prominent fishes seen in large stationary schools during the day are actually nocturnal species that leave the reef at dusk (Hobson 1968). Among these are croakers (Sciaenidae), snappers (Lutjanidae), and grunts (Pomadasyidae), which move to surrounding sand flats to feed on their invertebrate prey during the night (see papers by Hobson). However, we found no evidence of a pronounced nocturnal migration of fishes from reef and kelp to the surrounding sand. Essentially all of the fishes observed during the day were accounted for at one part or another of the reef at night. On several occasions at night, while swimming considerable distances over the surrounding sand flats, we saw only species that occur commonly at kelp-bed margins and do not actively forage at night (e.g., *Phanerodon furcatus* and *Damalichthys vacca*), or that typically inhabit sandy bottoms (e.g., the spotted cusk-eel *Chilara taylori*, and various skates and rays). We have occasionally seen relatively inactive schools of black croaker, *Cheilotrema saturnum*, on the reef during the day, and although we have not seen the fish at night, it is possible that they migrate to adjacent sandy areas to feed. Limbaugh (1961) reported that they are most active at night.

In a study of the night habits of coral reef fishes, Starck and Davis (1966) noted that the feeding times of reef fishes are closely related to the type and activities of their prey. Microcarnivorous and omnivorous fishes that browse and pick at sessile organisms are generally active only during the day. Mesocarnivorous fishes (i.e., those that feed on larger motile invertebrate prey) are largely nocturnal, because their prey (e.g., crustaceans) are active and exposed at night. Planktivorous fishes feed during both day and night, the nocturnal species having larger eyes than their diurnal counterparts. Piscivorous fishes feed opportunistically during the day and night, but are most active at dawn and dusk when their prey fish are exposed while moving to and from foraging and sheltering areas. This feeding pattern has also been observed in other tropical areas (Hiatt and Strasburg 1960; Collette and Talbot 1972; Hobson 1974) and in freshwater lakes (Emery 1973).

Kelp-bed fishes also tend to show this general feeding pattern, though perhaps not so distinctly. Small-mouthed microcarnivores that pick or graze sessile invertebrates and hidden prey from off the bottom and other substrates are generally active only during daylight hours. Such foragers, including most of the surfperches, as well as *Oxyjulis californica*, *Pimelometopon pulchrum*, and *Hypsypops rubicundus*, readily converge on urchins broken open during the day, but completely ignore such chum at night.

Also as in the tropics, though less extensively so, different planktivores feed in the mid-water zone of kelp beds during the day and night. The most visible daytime planktivores, *Chromis punctipinnis* and juvenile *S. mystinus*, often form mixed aggregations of individuals that pick small zooplankton from the incoming currents. At night, neither was seen exposed outside its shelter, and individuals collected by spear and later examined had empty stomachs. Instead, the mid-water zone is dominated at night by the large-eyed species, *Hyperprosopon argenteum*, which darts about, actively feeding throughout the water column. Though we have little data on kelp-bed mesocarnivores, some, such as various rockfishes, *Scorpaenichthys marmoratus*, and *Ophiodon elongatus*, may feed at night.

We emphasize the fact that many kelp-bed fishes show considerable intraspecific variability in vertical distribution and feeding activity. Although a large majority of the population of *C. punctipinnis* usually feeds in mid-water during the day, e.g., a few individuals can usually be found in holes. Likewise, a small proportion of the day-sampled individuals of *Embiotoca jacksoni* had empty foreguts even though the species is strictly a diurnal forager. Even more variable is the feeding schedule of *Rhacochilus toxotes*. Most individuals probably have empty guts at any daylight hour, although others are satiated. We have observed that at any given time during the day, most of these surfperch assemble as schools of varying sizes just above the bottom or even in mid-water (see also Alevizon 1975). However, a lone individual may suddenly leave the school to

feed rapidly over the bottom for several minutes before rejoining the same or another school of lazily swimming, nonfeeding fish. But we do not know yet if any particular individuals tend to feed in this sporadic manner during the day to a greater extent than do most others which may feed more consistently during the night. Hobson (1971, 1976) stressed the probably widespread occurrence of individual variation in the tendency of fishes to "clean" ectoparasites from larger host species. Specifically, Hobson (1976) observed that even though cleaning is not considered to be characteristic of the rock wrasse, *Halichoeres semicinctus*, this feeding mode was repeatedly a major activity in what was probably the same individual. Thus, as far as fish activities are concerned, the behavior of an individual is not always predictable from the general characteristics of its species.

Temperate-Tropical Differences

Some phenomena that characterize the day-night change in activities of fishes inhabiting tropical coral reefs appear less well developed or absent in the activity cycles of the Santa Barbara kelp-bed fishes. For one thing, no kelp-bed species that we observed forms inactive schools over the reef during the day and disperses elsewhere to feed at night, as do snappers and grunts in tropical systems. Another noticeable lack in the kelp forests is the widespread replacement of daytime mid-water planktivores by nighttime counterparts. In tropical areas, this replacement involves more species and, to some extent, occurs vertically: at night, the diurnal planktivores (a few pomacentrids, the unusual labrid *Clepticus*, etc.) take refuge in reefs that had provided shelter for the nocturnal planktivores (some holocentrids, apogonids, priacanthids, etc.) during the day (Hobson 1968, 1972; Collette and Talbot 1972). In our kelp-bed system at Naples Reef, however, the only noticeable replacement of the abundant daytime mid-water planktivores is *Hyperprosopon argenteum*, which, moreover, is probably a "horizontal replacement" from inshore areas. In this system, the only common fish that shelters during the day and may emerge at night is *Cephaloscyllium ventriosum*, a rather slow-moving piscivore that probably eats sheltering or inactive prey (Nelson and Johnson 1970). The cryptic demersal mesocarnivores (i.e., carnivores that feed on medium-sized prey, e.g., rockfishes, *Scorpaenichthys marmoratus*, etc.) may shelter either day or night between feeding bouts.

However, feeding on plankton at night may be more widespread in areas farther south. Hobson and Chess (1976) concluded that several species eat plankton at night off Santa Catalina Island. Though they are relatively rare at Naples Reef, for example, individuals of *Sebastes atrovirens* and larger juveniles of *S. serranoides* are important mid-water planktivores at night in kelp beds off Santa Catalina. Also, *Xenistius californiensis* picks plankton in the relatively clear waters around this island, but this species does not commonly occur as far north as Santa Barbara. Naples Reef is located just south of a faunal boundary at Point Conception (cf. Hubbs 1960; Quast 1968; Briggs 1974). Also, our mainland assemblage differs noticeably from nearby insular communities (Ebeling et al. unpubl. data). Nonetheless, it is reassuring to find that many of our results parallel those of Hobson and Chess.

Figure 2 summarizes the day-night distributions of kelp-bed fishes from an evolutionary point of view. Fish are depicted as being distributed vertically, based on their proportionate abundances in each of the four zones, from the mid-water zone to the shelter zone, and as comprising four ecological groups, based on their habits and phylogenetic origins. Belonging to taxa with temperate origins, all species in group A are demersal species of the bottom-habitat group, which generally move but little from their perches on the bottom during the day or night (see Table 4, $\bar{\Delta}h = 0.42$). Groups B, C, and D are composed of more active species that commonly occur in the suprabenthic zone and in mid-water during the day, but there the similarity ends. Also with temperate origins, species in group B are large-mouthed generalized predators, which can switch from plankton to larger prey including small fishes as the occasion arises (Love 1974), and simply descend to rest on the bottom at night ($\bar{\Delta}h = 1.92$). Group C and D species are small-mouthed microcarnivores of mixed origins, which either forage over the substrate or pick plankton from mid-water. Group C fishes are all surfperches with a common temperate origin, whose day-night change in vertical position is relatively slight ($\bar{\Delta}h = 0.22$), and whose nocturnal behavior is relatively unspecialized, in that the fish simply slow down over the bottom and do not generally seek shelter in holes and crevices. But in contrast with all the others, group D fishes appear to be rela-

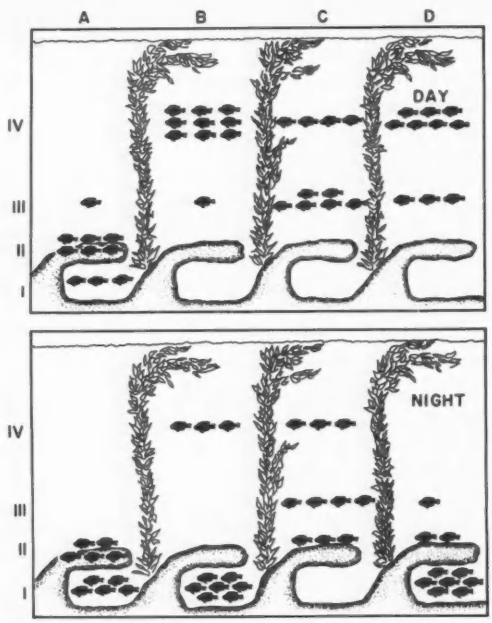

FIGURE 2.—Day and night positions of four ecological groups of fishes inhabiting Santa Barbara kelp beds: A) demersal species (*Coryphopterus nicholsii*, *Ophiodon elongatus*, *Oxylebius pictus*, *Sebastes carnatus*, *S. chrysomelas*, *S. serriceps*, and *Scorpaenichthys marmoratus*); B) large-mouthed generalized predators (*Paralabrax clathratus*, *Sebastes serranoides*, and adult *S. mystinus*); C) surfperches (*Embiotoca jacksoni*, *E. lateralis*, *Hypsurus caryi*, *Phanerodon furcatus*, *Rhacochilus toxotes*, and *Damalichthys vacca*); D) small-mouthed grazing and picking tropical derivatives (*Chromis punctipinnis*, *Hypsypops rubicundus*, *Medialuna californiensis*, *Oxyjulis californica*, and *Pimelometopon pulchrum*). Vertical zones (I-IV) are defined in Table 1. Each fish symbol represents 10% of the total individuals in the group expressed proportionally to the relative abundances of the different species in the group.

tively recent derivatives of primarily tropical families (Pomacentridae, Labridae, etc.), and essentially all show extreme changes in their vertical distribution ($\bar{\Delta}h = 2.07$) as they actively seek the shelter zone refuge. Some at least, like *Chromis punctipinnis*, are specialized to the extent that they tend to "home" to the same hole on successive nights (Bray unpubl. data).

Thus, in the kelp beds, there is no broad replacement for the "day shift" of fishes at night, even though the fishes' invertebrate prey appear to be more active and exposed then. And, in general, after the dusk period of intensified activity, the notably lackluster night life gives the kelp forest an aura of desolation, as compared with the pictures of renewed (albeit lessened) activity painted of the community of coral reef and outlying sand-flat fishes at night (Starck and Davis 1966; Collette and Talbot 1972; etc.). Perhaps the relatively clear and well-lighted tropical waters are more conducive to nocturnal activity for the many visually oriented fish. Denied much of the moonlight by the dense kelp canopy and frequent low clouds, the relatively turbid, temperate waters are often a dark and gloomy place at night. In fact, even during the day when the water is particularly turbid, the usually active planktivores, grazers, and browsers tend to stop foraging and often seek shelter, as do their tropical counterparts under similar conditions (Collette and Talbot 1972).

It is paradoxical that the "tropical derivatives" (Figure 2D) persist in their complex nocturnal shelter-seeking while many primarily temperate fishes remain exposed. One explanation assumes that selection pressures brought about by nocturnal (or crepuscular) predation are either different or more relaxed in our temperate system of kelp forest and reef than in the tropical reef system. Observing a similar set of circumstances, Hobson (1972) noted that Hawaiian reef fishes, which enjoy a relative dearth of crepuscular predators, show the same specialized sheltering behavior during twilight as do their close relatives in the Gulf of California, which have many such predators. He suggested that these complex behavior patterns may evidence historic selection pressures from predators. These patterns may persist on Hawaiian reefs today even though they are currently perhaps less critical to the survival of the refuge-seeking species than in reef systems elsewhere. An alternative explanation holds that crepuscular and nocturnal predation by, e.g., the Pacific electric ray, is important in kelp beds, but that the tropical derivatives compete more successfully against the primarily temperate species for shelter.

CONCLUSIONS

As indicated by paired day-night observations along a transect line, kelp-bed fishes occur in about the same relative abundances throughout the year in an area of reef and kelp along the mainland side of the Santa Barbara Channel. During the day, most fishes occupy the "mid-water zone" higher than 1 m off the bottom. Far fewer are "exposed on the bottom" or in the "shelter zone" of holes and crevices in the reef itself. During the night, when

the number of individuals appears reduced by more than half, most fishes occupy the bottom and shelter zones.

Thus, like that of tropical reefs, the vertical distribution of fishes changes markedly between day and night. Planktivores that pack the mid-water zone during the day virtually abandon the area at night to rest on the bottom or seek shelter in reef holes. The vacated mid-water space is only partly reoccupied by a relatively sparse population of nocturnal planktivores and a few remaining generalized carnivores. The largest relative increase of individuals occurs in the shelter zone, where superabundant daytime planktivores, such as the blacksmith, hide at night. With so many fishes commuting extensively between the mid-water and shelter zones, it is understandable that the intervening suprabenthic zone shows the greatest species similarity between day and night. Many ambusher-type foragers are always oriented to the bottom and change their positions relatively little for the night shift.

It seems likely, therefore, that at night feeding on plankton decreases and most of the foraging by fishes takes place over the bottom. The large-mouthed demersal ambushers—various rockfishes, the cabezon, and others—probably feed almost any time that suitable prey are available. The rubberlip seaperch may actually feed more actively at night. Nonetheless, many of the fishes that wander over the bottom at night may stop feeding at dusk. Most demersal surfperches remain exposed at night, although their foreguts soon empty, and the fish appear more lethargic than they do during the day when they are actively foraging.

Focal points of daytime fish activity, such as the productive crest of the reef and other prominent landmarks, appear to lose their attractiveness at night. Most aggregations disappear at dusk as fishes generally disperse out over the reef bottom. But unlike many tropical-reef fishes, kelp-bed species do not normally move off the reef to forage over the adjacent sand flats.

Kelp-bed fishes often show considerable intraspecific variation in vertical distribution and feeding activity. During the day, e.g., noticeable numbers of typically mid-water species invariably seek shelter, while at night some individuals remain in the water column. And fishes differ in the intensity at which they feed during any given period during the day. All this suggests that certain individuals may assume and even maintain distinctive habits that differ from the species "norm," i.e., the behavior of a particular fish is not always predictable from the general characteristics of its species.

Thus, in comparing the diel behavior of kelp-bed fishes as a group with that of their tropical counterparts, it becomes apparent that even though both groups follow the same basic patterns, the kelp-bed community is the more loosely "programmed." In the kelp-bed system, for example, there is less large-scale replacement of fishes between discrete areas or vertical zones at dusk. Here, the night shift offers no real substitute for the dense aggregations of daytime planktivores or demersal microcarnivores, even though these fishes' invertebrate prey are active and exposed at night. Perhaps the better lighted tropical waters allow more specialized activities because here the visually oriented fishes can better see what they are doing, even by moonlight. In the kelp forest, the level of fish activity decreases even during the day when the water becomes very turbid, as often happens with the onset of dense blooms of phytoplankton during the spring and summer.

The kelp-bed species that belong primarily to tropical families tend to show the same specialized pattern of nocturnal shelter seeking as do their close tropical relatives, even though the general program of diel activity in the kelp forest appears to be comparatively unstructured. Perhaps the specialized refuge-seeking procedures of kelp-bed pomacentrids and labrids are simply "evolutionary holdovers" that contribute relatively little to the present fitness of these fishes. But alternatively, the "tropical derivatives" may actually compete more successfully against primarily temperate species such as surfperches for shelter on the reef. Even though the intensity of predation at twilight and perhaps at dark may be somewhat less in our temperate system than in the tropics, a few ingenious and effective predators, such as the Pacific electric ray, patrol the Santa Barbara kelp forests throughout the night.

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LITERATURE CITED

ALEVIZON, W. S.
1975. Spatial overlap and competition in congeneric surfperches (Embiotocidae) off Santa Barbara, California. Copeia 1975:352-356.

BRAY, R. N., AND A. W. EBELING.
1975. Food, activity, and habitat of three "picker-type" microcarnivorous fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 73:815-829.

BRIGGS, J. C.
1974. Marine zoogeography. McGraw-Hill, N.Y., 475 p.

BROWN, D. W.
1974. Hydrography and midwater fishes of three contiguous oceanic areas off Santa Barbara, California. Los Ang. Cty. Mus. Contrib. Sci. 261:1-30.

CLARKE, T. A.
1970. Territorial behavior and population dynamics of a pomacentrid fish, the garibaldi, *Hypsypops rubicunda*. Ecol. Monogr. 40:189-212.

COLLETTE, B. B., AND F. H. TALBOT.
1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. *In* B. B. Collette and S. A. Earle (editors), Results of the Tektite program: Ecology of coral reef fishes, p. 98-124. Bull. Los Ang. Cty. Nat. Hist. Mus. Sci. 14.

COLWELL, R. K., AND D. J. FUTUYMA.
1971. On the measurement of niche breadth and overlap. Ecology 52:567-576.

DOMM, S. B., AND A. J. DOMM.
1973. The sequence of appearance at dawn and disappearance at dusk of some coral reef fishes. Pac. Sci. 27:128-135.

EMERY, A. R.
1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. J. Fish. Res. Board Can. 30:761-774.

FEDER, H. M., C. H. TURNER, AND C. LIMBAUGH.
1974. Observations on fishes associated with kelp beds in Southern California. Calif. Dep. Fish Game, Fish Bull. 160, 144 p.

FOLLETT, W. I., D. GOTSHALL, AND J. G. SMITH.
1960. Northerly occurrences of the scorpid fish *Medialuna californiensis* (Steindachner), with meristic data, life-history notes, and discussion of the fisheries. Calif. Fish Game 46:165-175.

FREY, H. W. (editor).
1971. California's living marine resources and their utilization. Calif. Dep. Fish Game Spec. Publ., 148 p.

GNOSE, E. C.
1968. Ecology of the striped seaperch, *Embiotoca lateralis*, in Yaquina Bay, Oregon. M.S. Thesis, Oregon State Univ., 51 p.

HERALD, E. S.
1961. Living fishes of the world. Doubleday and Co., Inc., Garden City, N.Y., 304 p.

HIATT, R. W., AND D. W. STRASBURG.
1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30:65-127.

HOBSON, E. S.
1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965:291-302.
1968. Predatory behavior of some shore fishes in the Gulf of California. U.S. Fish Wildl. Serv., Res. Rep. 73, 92 p.
1971. Cleaning symbiosis among California inshore fishes. Fish. Bull., U.S. 69:491-523.
1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull., U.S. 70:715-740.
1973. Diel feeding migrations in tropical reef fishes. Helgoländer wiss. Meeresunters. 24:361-370.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., U.S. 72:951-1031.
1975. Feeding patterns among tropical reef fishes. Am. Sci. 63:382-392.
1976. The rock wrasse, *Halichoeres semicinctus*, as a cleaner fish. Calif. Fish Game 62:73-78.

HOBSON, E. S., AND J. R. CHESS.
1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.

HUBBS, C. L.
1960. The marine vertebrates of the outer coast. *In* Symposium: The biogeography of Baja California and adjacent seas. Part 2, p. 134-147. Syst. Zool. 9.

KARIYA, T.
1969. The relationship of food intake to the amount of stomach contents in mebaru, *Sebastes inermis*. Bull. Jap. Soc. Sci. Fish. 35:533-536.

LARSON, R. J.
1972. The food habits of four kelp-bed rockfishes (Scorpaenidae, *Sebastes*) off Santa Barbara, California. M.A. Thesis, Univ. California Santa Barbara, 56 p.

LIMBAUGH, C.
1961. Life-history and ecologic notes on the black croaker. Calif. Fish Game 47:163-174.

LOW, R. M.
1971. Interspecific territoriality in a pomacentrid reef fish, *Pomacentrus flavicauda* Whitley. Ecology 52:648-654.

LOVE, M. S.
1974. Food habits of three midwater kelp-bed predators. M.A. Thesis, Univ. California Santa Barbara, 50 p.

MILLER, D. J., AND J. J. GEIBEL.
1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 158, 137 p.

NELSON, D. R., AND R. H. JOHNSON.
1970. Diel activity rhythms in the nocturnal, bottom-

dwelling sharks, *Heterodontus francisci* and *Cephaloscyllium ventriosum*. Copeia 1970:732-739.

QUAST, J. C.
1968a. Fish fauna of the rocky inshore zone. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in Southern California, p. 35-79. Calif. Dep. Fish Game, Fish Bull. 139.
1968b. Observations on the food of the kelp-bed fishes. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in Southern California, p. 109-142. Calif. Dep. Fish Game, Fish Bull. 139.
1968c. Observations on the food and biology of the kelp bass, *Paralabrax clathratus*, with notes on its sportfishery at San Diego, California. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in Southern California, p. 81-108. Calif. Dep. Fish Game, Fish Bull. 139.

SALE, P. F.
1972. Influence of corals in the dispersion of the pomacentrid fish, *Dascyllus aruanus*. Ecology 53:741-744.

SLOBODKIN, L. B., AND I. FISHELSON.
1974. The effect of the cleaner-fish *Labroides dimidiatus* on the point diversity of fishes on the reef front at Eilat. Am. Nat. 108:369-376.

SMITH, D. L., AND J. C. TYLER.
1972. Space resource sharing in a coral reef fish community. *In* B. B. Collette and S. A. Earle (editors), Results of the Tektite program: Ecology of coral reef fishes, p. 125-170. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 14.

STARCK, W. A., II, AND R. E. SCHROEDER.
1965. A coral reef at night. Sea Front. 11:66-79.

STARCK, W. A., II, AND W. P. DAVIS.
1966. Night habits of fishes of Alligator Reef, Florida. Ichthyol. Aquarium J. 38:313-356.

WILEY, J. W.
1974. Observations on the use of mucus envelopes by the California sheephead, *Pimelometopon pulchrum*, on southern California rock reefs. Copeia 1974:789-790.

INCIDENCE OF CULL LOBSTERS, *HOMARUS AMERICANUS*, IN COMMERCIAL AND RESEARCH CATCHES OFF THE MAINE COAST[1]

JAY S. KROUSE[2]

ABSTRACT

Data obtained by port sampling the Maine commercial lobster catch (1968-74) and the natural lobster population near Boothbay Harbor, Maine, with research gear (1969-74) indicate that 6.5% of the commercially harvested lobsters have lost at least one claw while 21.0% of the lobsters (all sizes) in the natural population have missing and/or regenerating claws. An assessment of variations in cull frequencies associated with different seasons, fishing localities, and lobster size distributions suggests a direct relationship between fishing intensity and the incidence of culls. This information further supports Krouse and Thomas' recommendation that all lobster traps be equipped with an escape vent thus minimizing fishermen's needless handling of excessive numbers of sublegal-sized lobsters.

Over the years the occurrence of American lobster, *Homarus americanus*, with a missing and/or regenerating cheliped in the commercial landings has undoubtedly resulted in a significant financial loss to the fishing industry due to the culls' reduced weight and marketability (retail price of culls is less per pound). Scarratt (1973) reported that commercially caught lobsters from ports off Nova Scotia and Prince Edward Island had incidences of missing claws ranging from 5 to 19%. Although claw loss could not be attributed to a single factor, causes related to fishing such as rough handling by fishermen and movement of traps over the seabed were cited. Recognizing the importance of this situation, I have analyzed cull data provided by the Maine Department of Marine Resources Lobster Research Program's research catches (Krouse 1973) and sampling of the commercial catch (Thomas 1973). In this paper I attempt to assess the magnitude of the cull problem along the Maine coast, some of its causes, and a possible solution to diminish the number of culls.

METHODS

From June 1969 through December 1974, the occurrence of lobsters with missing and/or regenerating claw(s) in daily catches of research gear was noted. Carapace length in millimeters, weight in grams, and sex were recorded for each lobster. Wire lobster traps (2.54 × 2.54 cm mesh) were fished throughout the 6-yr period, whereas modified wooden traps with plastic escape vents of 3.81, 4.13, and 4.45 cm were not used until July 1972. Most experimental fishing was conducted in the vicinity of Capitol, Squirrel, and Damariscove islands in the Boothbay region of Maine (Figure 1).

Information pertaining to the frequency of culls in the Maine commercial catch from 1968 through 1974 was obtained from the probability sampling program described by Thomas (1973).

A length-weight relationship was calculated for 297 lobsters with a regenerating claw and for 225 lobsters with a missing claw collected near Boothbay Harbor, 1972-73. All lobster culls used in this determination had one normal sized claw. The regression of weight on carapace length for these two cull categories was fitted by the method of least squares using the logarithmic transformation $\log_{10} W = \log_{10} a + b \log_{10} L$.

RESULTS AND DISCUSSION

Seasonal and Size Variation in Cull Frequency

From the research catches I have calculated the percentage of culls by month and 5-mm size groups for 1969 through 1974 (Tables 1, 2). Fluctuations in the monthly percentages of culls seem to follow a seasonal pattern, i.e., the number of culls peaked

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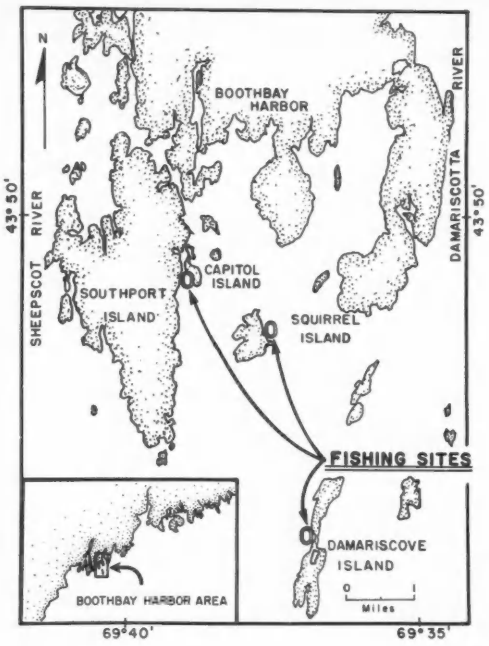

FIGURE 1.–Map showing the areas fished near Boothbay Harbor, Maine.

in the catch during winter-spring (26.9-31.3%), then subsided in July-August (18.1-19.4%), and increased in the fall (17.7-25.6%–variations in fall percentages may be due to sporadic shedding during this season). These seasonal changes might be related to the time of molting (July-September) associated with temporal fluctuations in fishing pressure. If we assume that a high percentage of the total number of culls are caused by fishing operations as suggested by earlier observations of fishermen's needless handling of excessive numbers of sublegal size lobsters (Krouse and Thomas 1975), then the decline in cull frequency during July and August (peak of shedding) may be explained, in part, by: 1) some culls losing this status after shedding and regenerating normal size claws, and 2) small lobsters (usually nonculls by virtue of their nonvulnerability to fishing gear) being recruited into the fishery at this time as a result of shedding. Even though the catch data of this study reveals that a high percentage of lobsters <45 mm carapace length were culls, most of these smaller culls probably acquired this condition while confined in our lobster traps.

TABLE 1.–Monthly incidence of lobster culls in research catches near Boothbay Harbor, Maine, 1969-74.

Month	Total no. examined	Culls (%)	Month	Total no. examined	Culls (%)
Jan.	16	31.3	Aug.	2,164	19.4
Feb.	26	26.9	Sept.	1,266	23.1
Mar.	34	29.4	Oct.	504	19.0
Apr.	83	26.5	Nov.	129	25.6
May	296	24.0	Dec.	62	17.7
June	805	24.0			
July	1,032	18.1	Total	6,417	21.0

TABLE 2.–Percentage of lobster culls by 5-mm size groups in research catches near Boothbay Harbor, Maine, 1969-74.

Carapace length (mm)	Total number caught	Culls (%)	Carapace length (mm)	Total number caught	Culls (%)
36- 40	19	26.3	76- 80	1,403	22.7
41- 45	77	33.8	81- 85	406	22.7
46- 50	160	21.9	86- 90	240	17.9
51- 55	333	19.5	91- 95	119	8.4
56- 60	542	23.2	96-100	20	10.0
61- 65	802	22.8	≥101	18	11.1
66- 70	1,046	19.3			
71- 75	1,232	19.2	Total	6,417	21.0

The frequency of culls by 5-mm increments (Table 2) indicated that culls are most prevalent at carapace lengths ≤45 mm and progressively less numerous at lengths ≥86 mm. The high incidence of culls for small lobsters can be attributed, at least in part, to these lobsters being particularly defenseless to claw loss inflicted by larger lobsters within the trap. On several occasions we have either caught small lobsters with recent claw losses in traps containing larger lobsters or actually witnessed larger lobsters destroying the claw of their diminutive opponent. To further substantiate this explanation of the two cull categories, i.e., regenerating and missing claws, the missing claw group predominated for lobsters ≤50 mm; however, for sizes ≥51 mm, lobsters with regenerating claws usually outnumbered those without claws (Table 3). This disparity was more pronounced for wood traps within the 81- to 85- and 86- to 90-mm groupings. Considering that legal-sized lobsters are handled only once and therefore are probably less prone to claw loss, then one would expect these larger lobsters to have a higher incidence of regenerating claws. Conversely, those sublegal-sized lobsters between 76 and 80 mm that are repeatedly discarded from the fishermen's catch have a preponderance of missing claws for catches with wire and wood traps.

The decline in the incidence of culls at the legal sizes (Maine minimum legal size is 81 mm carapace length) is manifested not only by the research

TABLE 3.–Percentage of lobster culls with missing claws by 5-mm size groups for research catches of wire and wooden traps.

Carapace length (mm)	Wire traps			Wood traps		
	Number of lobsters		Missing claw (%)	Number of lobsters		Missing claw (%)
	Regenerating claw	Missing claw		Regenerating claw	Missing claw	
36-40	2	3	60.0	—	—	—
41-45	2	15	88.2	—	—	—
46-50	7	15	68.2	—	—	—
51-55	15	15	50.0	—	—	—
56-60	50	34	40.5	—	—	—
61-65	62	45	42.1	—	—	—
66-70	65	51	44.0	2	8	80.0
71-75	74	55	42.6	16	15	48.4
76-80	57	74	56.5	59	66	52.8
81-85	14	17	54.8	30	17	36.2
86-90	4	2	33.3	20	10	33.3
≥91	1	1	50.0	5	5	50.0
Total	353	327	48.1	132	121	47.8

catches (Table 2) but also by the commercial catches for 1968-74 (Table 4). For both catches, more legal-sized culls occurred in the 81- to 85-mm size group while the percentage of culls gradually decreased for carapace lengths >85 mm. If, once again, it is assumed that fishing operations often cause culled lobsters and knowing that legal lobsters are handled only once and not repeatedly as may be the case for sublegal-sized lobsters, one would expect fewer culls amongst legal lobsters along with a gradual reduction in culls for sizes >85 mm. Since this study's data demonstrate this very pattern, my contention concerning the possible injurious effects of fishing activities on lobsters <81 mm is strengthened. Certainly there is a greater likelihood of a lobster becoming injured when as a result of fishing operations this lobster is: 1) crowded with other cannibalistic lobsters in a trap; 2) held captive in a trap which may undergo rigorous movement during a storm; 3) hauled boatside with appendages dangling between the trap's laths; and 4) removed from the trap while clinging to the trap, fishermen, or another lobster and eventually released for a descent to the ocean floor during which predation may occur.

TABLE 4.–Incidence of lobsters with missing claws by 5-mm size groups occurring in the commercial catch along the Maine coast (1968-74).

Carapace length (mm)	Total number caught	Culls (%)	Carapace length (mm)	Total number caught	Culls (%)
81- 85	5,322	8.1	106-110	219	3.7
86- 90	7,373	6.2	111-115	109	1.8
91- 95	5,580	5.2	116-120	41	4.9
96-100	1,208	3.7	≥121	6	0
101-105	368	4.3	Total	20,226	6.5

Effect of Fishing Intensity on Cull Frequency

The relationship of fishing intensity and its influence on cull incidence was investigated by calculating the frequencies of culls caught with wire and wood lobster traps (Table 5) at three different fishing sites near Boothbay Harbor (Figure 1). In addition, length-frequency histograms were constructed by 1-mm increments of the catches for each of the sampling sites (Figure 2). This analysis revealed that catches off Capitol Island, the most intensively fished area, contained more culls (23.3% for wire and 22.0% for wood traps) than either the catch of Damariscove (21.2%) or Squirrel islands (12.7% for wire and 17.9% for wood traps) which had the fewest culls. Although Damariscove and Squirrel islands appeared to have similar trap concentrations based on visual sightings of pot buoys, appreciably more culls were trapped at Damariscove. Possible reasons for this difference may be related to: 1) lobsters being maimed by excessive movement of traps over the substrate during storms off the more exposed seaward shoreline of Damariscove (waters fished at Squirrel were more sheltered); 2) Damariscove's greater abundance of small lobsters which are more vulnerable to injury [average size of lobsters in Damariscove catch was smaller than those of the other two areas (Figure 2), and the percentage of lobsters with missing claws was highest at Damariscove (Table 5)]; and 3) perhaps, an error in our rather subjective determination of nearly equal fishing intensities for both islands. Nevertheless, there does appear to be a positive

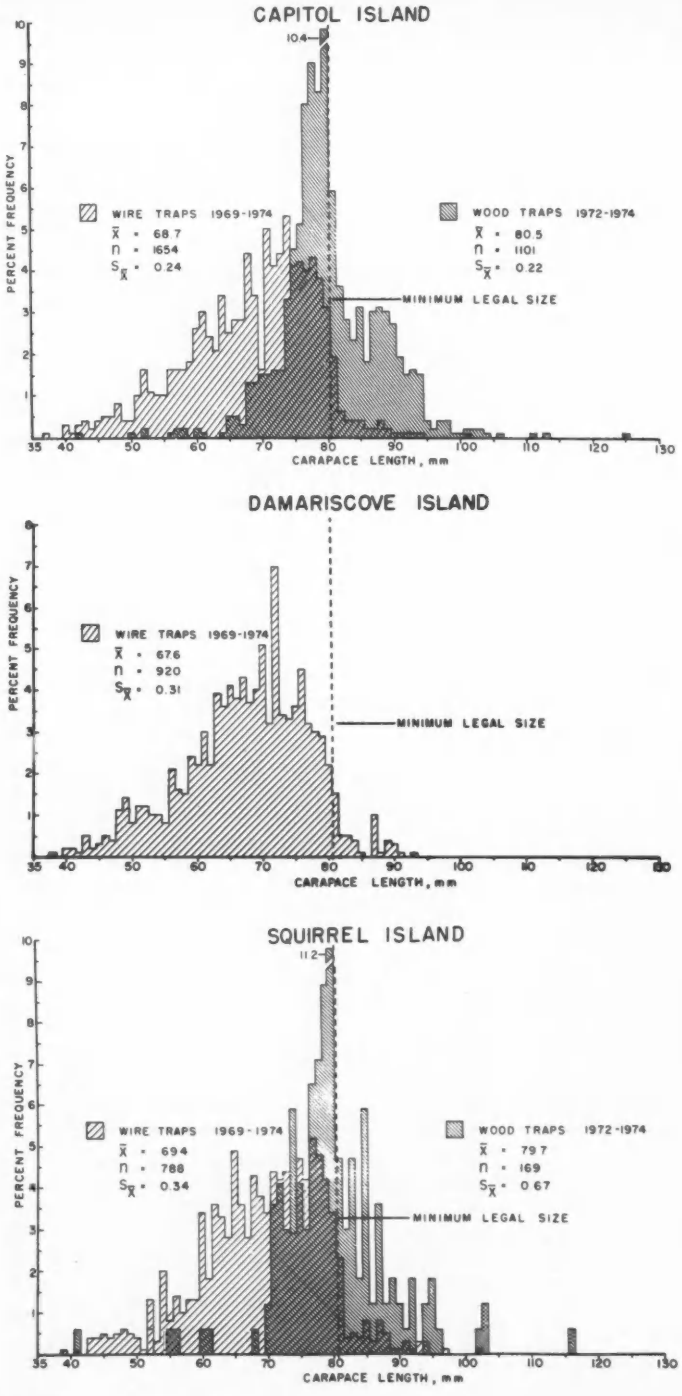

FIGURE 2.—Length-frequency histograms for the lobster catches with wire and wood traps for each of the three sampling sites near Boothbay Harbor, Maine.

TABLE 5—Comparison of the incidence of lobster culls in catches of wire and wood traps for various areas near Boothbay Harbor, Maine, 1969-74.

Gear and area	Total no. lobsters	Culls (%)	Regenerating claw (%)	Both claws regenerating (%)	Missing claw (%)	Both claws missing (%)	Regenerating and missing claws (%)
Wire traps:							
Capitol	1,627	23.3	10.6	1.8	9.1	1.1	0.7
Damariscove	920	21.2	8.4	1.0	10.0	1.0	0.5
Squirrel	787	12.7	6.9	0.5	5.1	0.1	0.1
Wood traps:							
Capitol	1,125	22.0	10.0	1.4	8.4	1.3	0.8
Squirrel	162	17.9	8.6	1.9	5.6	1.9	0

correlation between fishing intensity and incidence of culls; however, this does not preclude other factors such as predation, intraspecific competition, molting difficulties, and storm related damages.

Loss of Value of Catch Due to Culls

At the beginning of this paper I mentioned that culls have perennially detracted from the landed value of the lobster catch. To assess this situation, the regressions of weight for lobsters with missing and regenerating claws on carapace length for sublegal- and legal-sized lobsters were calculated. These curves were then compared to the length-weight relationship for noncull lobsters (Krouse 1973) (Figure 3). These comparisons reveal that noncull lobsters are about 14 to 20% heavier than those lobsters with regenerating and missing claws. Knowing these weight differentials and that about 6.5% of the lobsters in the commercial catch are missing at least one claw (Table 4) and that at least an equal percentage (6.5) of lobsters must have regenerating claws, the cull loss to the fishery can now be quantified. From the 1974 Maine Landings which reported a lobster catch of 16,457,666 pounds valued at $23,212,808, I estimated that the annual catch without any culls could have been increased by about 363,700 pounds (2.2%), adding $512,800 to the landed value. Unfortunately, there probably is no way to eliminate culls completely; however, proper size escape vents in all traps would be beneficial in effecting a marked reduction in the incidence of culls (Krouse and Thomas 1975). This reduction in culls would be the result of decidedly fewer numbers of sublegal-sized lobsters being handled by fishermen as indicated by the conspicuous disparity between the size composition of research catches with wire and vented wooden traps (Figure 2). Even if the cull loss could be lessened by only 25%, the industry would still realize an annual increase of about $128,000.

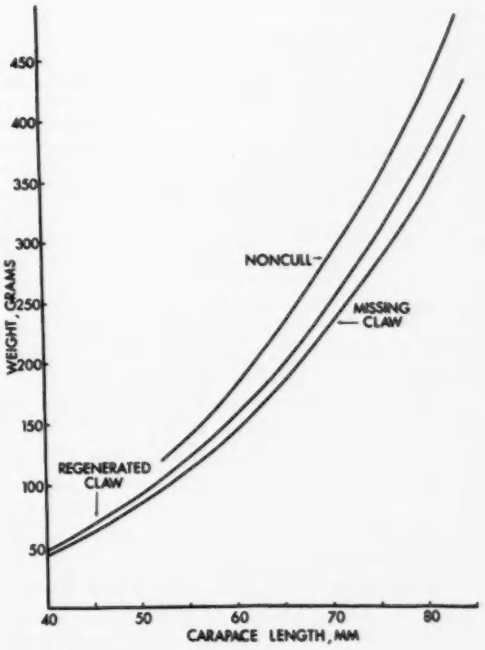

FIGURE 3.—Comparison of the calculated length-weight relationships for lobsters with regenerating, missing, and normal claws (noncull). The regression equations are: 1) regenerating claws: $\log_{10} W = -2.99 + 2.91 \log_{10} L$; 2) missing claws: $\log_{10} W = -3.03 + 2.92 \log_{10} L$; and 3) noncull: $\log_{10} W = -2.91 + 2.90 \log_{10} L$.

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LITERATURE CITED

KROUSE, J. S.
1973. Maturity, sex ratio, and size composition of the natural population of American lobster, *Homarus americanus*, along the Maine coast. Fish. Bull., U.S. 71:165-173.

KROUSE, J. S., AND J. C. THOMAS.
1975. Effects of trap selectivity and some population parameters on size composition of the American lobster, *Homarus americanus*, catch along the Maine coast. Fish. Bull., U.S. 73:862-871.

SCARRATT, D. J.
1973. Claw loss and other wounds in commercially caught lobsters *(Homarus americanus)*. J. Fish. Res. Board Can. 30:1370-1373.

THOMAS, J. C.
1973. An analysis of the commercial lobster *(Homarus americanus)* fishery along the coast of Maine, August 1966 through December 1970. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-667, 57 p.

FISHERY WASTE EFFLUENTS: A METHOD TO DETERMINE RELATIONSHIPS BETWEEN CHEMICAL OXYGEN DEMAND AND RESIDUE

JEFF COLLINS AND RICHARD D. TENNEY[1]

ABSTRACT

Researchers and the fishing industry have experienced difficulty in applying the Environmental Protection Agency's standard tests to industrial fishing waste effluents, especially for total suspended and settleable solids, and oil and grease.

The relationship between chemical oxygen demand and residue was determined on a limited number of samples from four types of screened waste effluents from November 1973 to September 1974: shrimp using fresh or salt water processing, snow crab, and canned salmon. In addition to chemical oxygen demand and residue, tests for settleable solids, total suspended and settleable solids, oil and grease, protein, and salt were also performed. Based on these relationships, a method is suggested to develop a system for the analysis of pollutants that will be more economic and give more meaningful data than currently obtainable under Environmental Protection Agency's methods. The method requires that base data on a plant be obtained to relate chemical oxygen demand with residue values using regression lines and equations. A subsequent routine monitoring program need only test for total residue and chemical oxygen demand of the filterable residue. Substitution into the equations gives the other residue fractions and their chemical oxygen demand values, i.e., total chemical oxygen demand, chemical oxygen demand of the particulate matter, filterable residue, and nonfilterable residue.

This laboratory has modified and studied in detail a number of analytical techniques to measure pollutants (Tenney)[2]. We have considered the methods of testing specified by the Environmental Protection Agency (EPA) to monitor fishery pollutants and are of the opinion that the monitoring program and analytical methods specified under the National Pollutant Discharge Elimination System (NPDES) program could be improved for application to seafood-processing effluents (Pojasek 1975). The purpose of this paper is to suggest different tests for monitoring effluents with certain prerequisites that would satisfy the intent of the law, yet recognize both the technical and economic problems associated with the fishing industry's efforts to comply with the monitoring regulations.

Since laboratory space, equipment, and labor necessary to conduct a waste-monitoring program are quite expensive to the fishing industry, economics suggest the use of a minimum number of tests to do the job, and where possible, the use of inexpensive equipment. In some analyses, the time required to complete any analysis is important, as in the 5-day test for biological oxygen demand (BOD). In this instance, the chemical test (chemical oxygen demand–COD) provides quick results and has better application. The limited level of laboratory experience and equipment generally found in seafood-processing plants and their diverse and often remote locations also suggest that the regulations and permit system should reflect these limitations and require only fairly simple tests to measure pollutants. At the same time, however, analytical techniques used to measure pollutants must be accurate, have good precision, and be a meaningful measure of pollutants.

In this study we have evaluated the relationship between COD and residue of the screened effluents of four plants. Based on these correlations, a monitoring system is suggested that enables the results of two analyses to provide data on six pollutant parameters.

EXPERIMENTAL

Identification and Definition of Terms

BOD (*Biochemical oxygen demand*): oxidation by bacteria.

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[2]Tenney, R. D. 1972. COD for Industrial Waste Water, Tech. Rep. 97, 5 p.; 1972. Chemical Oxygen Demand, Tech. Rep. 101, 12 p.; 1973. Shrimp Waste Streams and COD, Tech. Rep. 104, 3 p. Unpublished, intralaboratory reports, Kodiak Utilization Research Laboratory.

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COD (*Chemical oxygen demand*): oxidation by potassium dichromate.

Residue: This term does not necessarily mean solids, rather it is the results of or the substance remaining from a separation process such as filtering or drying. For example, if a solvent is evaporated from oil, the resulting residue is a liquid, not a solid.

TR (*Total residue*): is the weight of material remaining from a sample of the original screened effluent after overnight drying at 103°C.

FR (*Filterable residue*): is the residue of the filtrate (GF/A glass filter) dried at 103°C. Drying seafood effluents at 180°C (Environmental Protection Agency 1974) produced results that could not be related to the TR and nonfilterable residue.

NFR (*Nonfilterable residue*): is the residue remaining on the glass filter after drying at 103°C. Since the three residue terms are related and provided drying conditions are the same, NFR can be determined indirectly, i.e., TR - FR.

SS (*Settleable and floatable solids*): This term has caused considerable trouble to the industry and researchers. By custom, the volume of the settled portion in the Imhoff cone is measured and considered SS. However, this measurement does *not* actually measure SS, because floatables are not included in the reading. The term only has correct meaning when SS is determined in milligrams/liter by difference: the NFR minus the NFR of a sample taken from near the center of the Imhoff cone after 1 h of settling.

Sus. Sol. (*Suspended solids*): are the particulate matter suspended in the center of the Imhoff cone, i.e., the NFR of that area.

TSS (*Total suspended nonfilterable solids*): This term has also caused confusion. It means the dry weight of all particulate matter (settleable, suspended, floatable), i.e., the NFR. For both technical and grammatical reasons, NFR is the preferred term.

O&G (*Oil and grease*): content was determined by a method in which the precipitated, filtered-solids material plus Celite[3] (used as a precipitation aid) is extracted directly under anhydrous conditions, using 2-propanol and petroleum ether (Collins 1976). This technique extracts all lipidlike material, including carotenoids.

Protein: The nitrogen content was determined by the macro-Kjeldahl method on 100- to 200-g samples and expressed as protein by multiplying N by 6.25 (Horwitz 1965:273).

Salt: Chloride was determined by the standard $AgNO_3$ method and expressed as NaCl (Horwitz 1965:273).

Subscripts: In this paper, we use subscripts to identify the particular portion of the sample tested. For example, COD_{TR} is the COD of the screened waste effluent, and COD_{FR} is the COD of the FR, i.e., the filtrate, not the actual dried FR. If no subscript is used, we are referring to the test in general or to the test on the original screened sample, i.e., COD is the same as COD_{TR}.

Industrially screened shrimp and crab effluents were obtained from November 1973 through February 1974 and from salmon effluents July through September 1974. Since our purpose was to compare data rather than characterize the level of pollution in a plant, we took grab samples at specific times during the production to get a useful range of values. The following analyses were made: COD_{TR}, COD_{FR}, TR, FR, NFR (i.e., TSS), SS, protein, O&G, salt, and the COD of a sample from the center of the Imhoff cone after 1 h of settling.

In conducting these analyses we used the methods of the Environmental Protection Agency (1974), unless otherwise indicated. The particulate matter in our samples of fishery waste was so high that the filter clogged frequently before the entire sample had been filtered. For this reason, sample sizes were reduced, where necessary, to 25 ml.

The degree of pollutant in an effluent is affected by the processes employed, species processed, and the use of fresh or salt water in varying degrees during processing. Mechanical shrimp peelers use about 7 gallons of water per pound of shrimp. Salt water from wells close to the shore or from the ocean is sometimes used on the mechanical peelers. The two main types of peelers vary in their relative waste load. The Model A peeler peels raw shrimp and generally has a higher waste load than the Model PCA peeler that peels a steam-blanched shrimp.

RESULTS

Study 1—Shrimp: Analyses of effluents from a shrimp plant processing with fresh water and mechanical peelers (Model A).

Over a 10-day period in December 1973, eight samples of waste effluents were taken from the underflow of the Bauer Hydrasieve (tangential screen, 0.04-inch) and analyzed (Table 1). Averages for COD by analysis are as follows:

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

a. COD, screened effluent 3,257 mg/liter
b. COD, center of Imhoff cone 3,043 mg/liter
c. COD, filtrate of NFR test 1,616 mg/liter

By calculation, the COD of the particulate matter and its percentage contribution to the total COD are:

COD of NFR (a - c) = 1,641 mg/liter 50.4%
COD of SS by weight
(a - b) = 214 mg/liter 6.6%
COD of Sus. Sol.
[(a - c) - (a - b)] = 1,426 mg/liter 43.8%

By analysis and calculation, data were also obtained for the means of other residue tests:

By analysis:
d. Total residue (TR) 2,381 mg/liter
e. Filterable residue (FR) 1,577 mg/liter
f. Settleable solids (SS) 5.6 ml/liter
g. Nonfilterable residue (NFR) 769 mg/liter

By calculation: NFR, i.e., (d - e) or TR - FR = 804 mg/liter.

By weight, the FR was 66.3% of the TR, but the COD of the FR was only 49.6% of the total COD. The NFR, however, contributed only 33.7% to the TR by weight but contributed 50.4% as COD.

The standard deviations (SD) in Table 1 show relatively large values in agreement with practical experience. The higher average concentration and lower SD for the NFR determined by difference suggests that this is a better method for determining the concentration of NFR than is the direct analysis.

Study 2—Shrimp: Analyses of effluents from a shrimp plant processing with salt water and mechanical peelers (Models A and PCA).

Ten samples of waste effluent were taken from the underflow of the 0.7-mm Dorr-Oliver screen. The individual results are given in Table 2, and the average analytical data are as follows:

a. COD, screened effluent 2,643 mg/liter
b. COD, center of Imhoff cone 2,338 mg/liter
c. COD, filtrate from NFR test 1,519 mg/liter
d. Settleable solids (SS) 7.8 ml/liter
e. Nonfilterable residue (NFR) 684 mg/liter

TABLE 1.—Analyses of shrimp waste effluents from a plant processing with fresh water and mechanical peelers (Model A). All values are in milligrams per liter except SS in milliliters per liter.

Date of sample	Screened effluent		Filtrate (glass filter)		By difference		Center Imhoff	SS	Direct analysis
Dec. 1973	COD_{TR}	TR	COD_{FR}	FR	COD_{NFR}	NFR	COD	Vol	NFR
11	3,070	2,370	1,492	1,640	1,578	730	2,856	8.0	880
12	3,364	2,660	2,040	1,990	1,324	670	3,212	7.0	840
13	3,068	2,290	1,580	1,540	1,488	750	2,912	3.0	656
14	2,516	1,970	1,240	1,350	1,276	620	2,312	7.0	796
18	3,353	2,280	1,405	1,360	1,948	920	2,956	11.0	892
19	2,660	1,790	1,080	1,010	1,580	780	2,418	2.0	120
20	2,962	2,040	1,588	1,420	1,374	620	2,841	2.5	660
21	5,065	3,650	2,500	2,310	2,565	1,340	4,836	4.0	1,308
Mean	3,257	2,381	1,616	1,577	1,642	804	3,043	5.6	769
SD	789	578	455	407	428	238	781	3.2	332

TABLE 2.—Analyses of shrimp waste effluents from a plant processing with salt water and mechanical peelers (Models A and PCA). All values are in milligrams per liter except SS in milliliters per liter.

Date of sample	Screened effluent		Filtrate (glass filter)		By difference		Center Imhoff	SS	Direct analysis
	COD_{TR}	TR	COD_{FR}	FR	COD_{NFR}	NFR	COD	Vol	NFR
18 Nov. 1973	3,264	33,500	—	—	—	—	2,915	8.0	993
27 Nov.	4,050	—	2,690	—	1,360	—	3,883	3.0	—
7 Dec.	2,090	25,550	1,212	25,360	878	190	1,882	4.0	580
10 Dec.	3,161	34,090	1,729	33,780	1,432	310	2,935	9.0	1,212
2 Jan. 1974	3,143	27,730	1,733	—	1,410	—	2,849	8.0	1,008
9 Jan.	2,364	23,314	1,353	—	1,011	—	2,021	9.0	180
1 Feb.	2,890	23,300	1,363	23,100	1,527	200	2,487	10.0	616
4 Feb.	1,948	26,610	1,100	—	848	—	1,640	9.5	476
7 Feb.	2,442	23,940	1,659	—	783	—	1,806	9.5	896
15 Feb.	1,080	25,240	828	25,200	252	40	960	8.0	192
Mean	2,643		1,519		1,056		2,338	7.8	684
SD	836		534		415		839	2.4	367

By calculation, the COD of the particulate matter and its percentage contribution to the total COD are:

COD of NFR	(a - c) =	1,124 mg/liter	42.5%
COD of SS	(a - b) =	305 mg/liter	11.5%
COD of Sus. Sol. [(a - c) - (a - b)]	=	819 mg/liter	31.0%

Some figures were also collected on the concentration of residues by direct analysis and are included in the table to illustrate the problems associated with monitoring plants that process with salt water. Residue values were not determined by calculation because of the high and variable salt content. It is questionable that meaningful data for NFR can be obtained because of errors that can occur when the salt values of about 25,000 mg/liter are subtracted from the mean TR values of about 27,000 mg/liter.

Study 3—Snow Crab: Analyses of effluents from a plant processing both meats and sections in fresh water.

Over a 2-wk period in February 1974, six samples of waste effluent from a plant processing snow crab using fresh water were taken from the underflow of Dorr-Oliver 0.4-mm screen and analyzed (Table 3). Average values by analysis are as follows:

a.	COD, screened effluent	1,426 mg/liter
b.	COD, center of Imhoff cone	1,332 mg/liter
c.	COD, filtrate from NFR test	824 mg/liter
d.	Total residue (TR)	1,393 mg/liter
e.	Filterable residue (FR)	1,086 mg/liter
f.	Settleable solids (SS)	4.2 ml/liter
g.	Nonfilterable residue (NFR)	277 mg/liter

By calculation, the mean values for COD of the particulate matter and its percentage contribution to the total were:

COD of NFR	(a - c) =	602 mg/liter	42.2%
COD of SS	(a - b) =	94 mg/liter	6.6%
COD of Sus. Sol. [(a - c) - (a - b)]	=	503 mg/liter	42.2%

By calculation, the mean value for NFR is: (d - e) = 307 mg/liter.

Study 4—Salmon: Analyses of effluents from a plant processing canned salmon.

During the summer of 1974, ten samples of

TABLE 3.—Analyses of snow crab waste effluents from a plant processing both meats and sections in fresh water. All values are in milligrams per liter except SS in milliliters per liter.

Date of sample Feb. 1974	Screened effluent		Filtrate (glass filter)		By difference		Center Imhoff	SS	Direct analysis
	COD_{TR}	TR	COD_{FR}	FR	COD_{NFR}	NFR	COD	Vol	NFR
6	680	880	506	770	174	110	599	1.3	126
8	888	960	650	650	238	110	868	0.5	41
11	1,056	1,230	746	1,030	310	200	974	5.0	143
14	1,560	1,590	870	1,280	690	310	1,408	4.0	462
19	1,988	1,900	1,077	1,500	911	400	1,889	7.5	540
25	2,383	1,800	1,093	—	1,290	—	2,254	7.0	348
Mean	1,426	1,393	824	1,086	602	226	1,332	4.2	277
SD	668	433	235	303	442	127	640	2.9	202

TABLE 4.—Analyses of salmon waste effluents from a plant processing canned salmon. All values are in milligrams per liter.

Date of sample 1974	Salmon	Screened effluent					Filtrate — glass filter				By difference	
		COD_{TR}	TR	Protein	O&G	Salt	COD_{FR}	FR	Protein	Salt	COD_{NFR}	NFR
30 June	Red	5,716	3,695	2,197	1,190	574	1,365	1,513	1,044	545	4,351	2,182
7 July	Red	2,908	2,076	1,500	330	373	1,212	1,135	656	273	1,696	941
8 July	Red	4,069	2,368	1,453	918	253	1,131	1,078	744	247	2,938	1,290
11 July	Chum	2,070	1,125	1,179	308	—	797	350	531	453	1,273	775
14 July	Chum	6,294	4,450	2,980	—	728	2,687	2,560	1,775	436	3,607	1,890
17 July	Pink	9,513	7,102	—	—	596	4,020	3,655	3,346	465	5,493	3,447
30 July	Chum	9,101	6,315	3,346	1,407	397	3,420	2,813	—	—	5,681	3,502
13 Aug.	Pink	5,236	3,595	2,378	845	493	1,462	1,465	1,009	459	3,774	2,130
14 Aug.	Pink	2,647	2,148	1,518	226	344	1,822	1,570	1,168	292	825	578
22 Aug.	Mixed	6,219	4,874	3,263	924	542	2,615	2,722	1,938	556	3,604	2,152
Mean		5,377	3,775	2,201	769	489	2,053	1,886	1,357	414	3,324	1,889
SD		2,557	1,937	840	437	157	1,078	1,007	885	115	1,664	1,026

salmon cannery waste effluent were taken from the underflow of a Bauer screen (0.03-inch) (Table 4). The average values by analysis and calculation are as follows:

a.	COD, screened effluent	5,377 mg/liter
b.	COD, filtrate of NFR test	2,053 mg/liter
c.	COD, of NFR (a - b)	3,324 mg/liter
d.	Total residue	3,775 mg/liter
e.	Filterable residue	1,886 mg/liter
f.	Nonfilterable residue (d - e)	1,889 mg/liter
g.	O&G, screened effluent	769 mg/liter
h.	Protein, screened effluent	2,201 mg/liter
i.	Salt, screened effluent	489 mg/liter

The NFR is 50% of the TR, but the COD of the NFR is 62% of the total COD.

DISCUSSION

The following discussion is concerned with monitoring parameters previously suggested or currently in effect under EPA effluent limitations for seafood processing and with the suggestion of a more precise and simpler monitoring system. The present EPA requirements, however, for use of alternative analytical methods must be considered. Under EPA rules (Title 40 "Code of Federal Regulations," Parts 136.4 and 136.5), any person wishing to use alternative analytical methods for the parameters listed must follow variance procedures specified under the NPDES permit system.

Current permits require monitoring for SS, COD (i.e., COD_{TR}), TSS (i.e., NFR), O&G, flow, and pH. SS is imprecise and contributes so little to the pollution load in seafood processing that it has relatively little value as a measure of pollution, although it has merit as a check on the efficiency of screen operation. As discussed later, total COD can be determined more accurately in an indirect manner. The O&G analysis is difficult to do, and this value, too, can be obtained more accurately through calculation. Data in this paper suggest that the indirect analysis for NFR (i.e., TSS) was more accurate than the direct method. The FR is an important parameter because this fraction contributed about 50% to the total COD or TR and will need to be considered in the design of future treatment systems.

To develop an improved monitoring system, we plotted the COD and residue data of Table 1 to illustrate the correlation between the COD of the residue and the concentration of the residue (Figure 1). The regression lines and equations were determined by the method of least squares. The TR and FR regression lines were obtained through direct analyses, and the NFR line was obtained by difference. The maximum deviation of any COD value from the regression line was 260 mg/liter. This is slightly less than the possible error of the analytical method (± 8%) (Moore et al. 1949). On the average, the individual values were within 107 mg COD of the regression line.

The correlations shown in Figure 1 can be used to calculate COD and residue values. In the following, the first three equations are the regression lines of Figure 1 and the next three are derived equations to solve for residue rather than for COD. Of course, these equations are valid only for this group of data and for this particular plant. If the TR and COD_{FR} are determined by analysis, the other values can be derived from the equations or the regression line and from the expression TR = FR + NFR.

$$COD_{TR} = 1.32\,TR + 113 \quad (1)$$
$$COD_{FR} = 1.08\,FR - 96 \quad (2)$$
$$COD_{NFR} = 1.78\,NFR + 210 \quad (3)$$

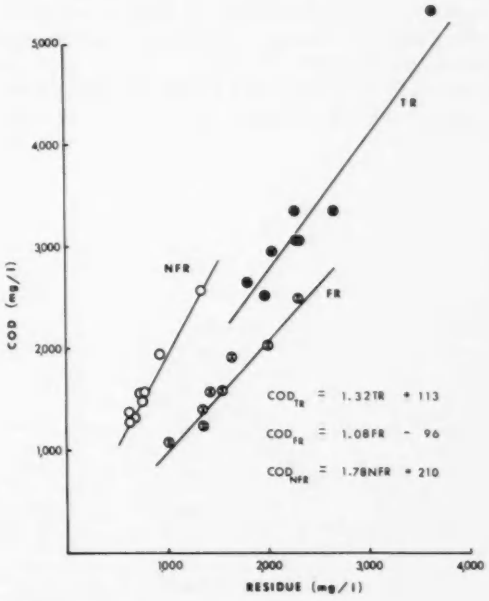

FIGURE 1.—Relationship between the COD of the residue and the concentration of the residue from shrimp processed on Model A peelers using fresh water.

$$TR = 0.76\ COD_{TR} - 86 \quad (4)$$
$$FR = 0.93\ COD_{FR} - 89 \quad (5)$$
$$NFR = 0.56\ COD_{NFR} - 118 \quad (6)$$

When salt water was used in processing, such as in the second plant study (Table 2), the residue values included salt. Since salt values were not determined, COD and residue data were not correlated for this plant.

In the third plant study of snow crab effluent, the data (Table 3) were plotted similarly to the shrimp data (Figure 2). The basic equations for snow crab can also be used to calculate from two analyses the other COD or residue values. The equations are listed in Figure 2.

Data for the fourth plant study of salmon-waste effluents (Table 4) were also plotted, and the regression lines and equations were similarly determined (Figure 3). The regression lines for salmon are less precise because of the variable salt content of the effluent and the high levels of COD and residue. Salt varied because of the erratic operation of the salmon egg-processing room. These regression lines (salmon) should not be used to calculate or interpolate COD or residue values unless a check is first made on salt content. If salt content of the effluent is about normal (500 mg/liter), the calculation is valid since these equations are derived from data with a high standard deviation for salt. A check is made to ensure that the level is not 1 or 2% as it could be if a brine tank were dumped. A routine composite sampling program for the plant, of course, would reduce salt variation.

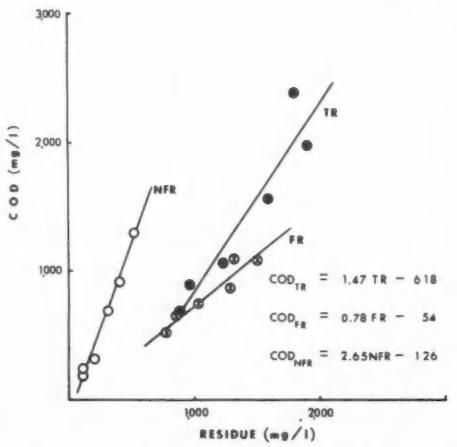

FIGURE 2.—Relationship between the COD of the residue and the concentration of residue from the processing of snow crab meats and sections.

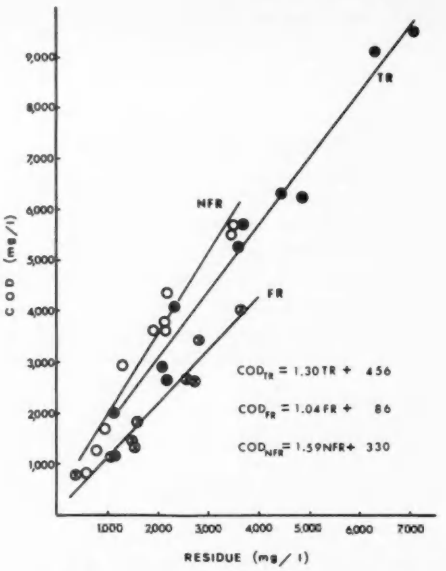

FIGURE 3.—Relationship between the COD of the residue and the concentration of the residue for canned salmon processing.

A SIMPLIFIED MONITORING SYSTEM

The data of the first plant study (Table 1) and the six equations listed earlier may be used to illustrate how a simplified monitoring system can be set up for a particular plant.

Since COD is difficult to determine on the original effluent (particulate matter causes dilution problems) and impractical to determine on a solid sample, COD should be determined on the filterable residue sample before drying. Equation (5) is then used to calculate FR in milligrams per liter. It is not necessary to actually finish the FR test. The next analysis most logically should be the total residue test. It is an easy test to do and is accurate. Equation (1) is used to calculate the COD of the TR, and the previously calculated FR is subtracted from TR to give the NFR in milligrams per liter. Equation (3) is then used to calculate the COD of the NFR. Thus, two analyses plus several calculations give three COD and three residue values.

The two analyses recommended (COD_{FR} and TR) are logically the most accurate of the six

possible, thus the other calculated values that are based on an ideal regression line should be more valid than those obtainable by direct analysis. Although this system may suggest doing the FR rather than the COD_{FR}, we believe that one direct analysis for COD is desirable, since the effect of oxygen demand on the receiving water is an important parameter of a monitoring program. Although O&G were not specifically considered except for salmon, for which we had limited data, the COD and residue data imply that O&G are related and that a regression line could be calculated.

In conclusion, it appears that in-plant monitoring for COD_{FR} and TR and the application of proper correlation factors and equations previously determined for the plant effluent will give reportable data on COD_{TR}, COD_{NFR}, COD_{FR}, TR, FR, and NFR. The suggested analyses can be done at reasonable cost with simple equipment, are capable of good precision and accuracy, and can be conducted by quality assurance personnel in the fishing industry. We suggest, recognizing the limitations of our data and obvious and known differences between processing plants and processing methods, that if regression lines or correlations similar to those given in this paper were determined, the resulting monitoring system would be simpler and more accurate than that currently in use.

In a subsequent paper, we will report regression data for protein and O&G similar to that suggested in this paper and a method using a simultaneous equation to calculate protein and O&G from TR and COD data.

LITERATURE CITED

COLLINS, J.
1976. Oil and grease: A proposed analytical method for fishery waste effluents. Fish. Bull., U.S. 74:

ENVIRONMENTAL PROTECTION AGENCY.
1974. Methods for chemical analysis of water and wastes. Environ. Prot. Agency, Off. Tech. Transfer, Meth. Dev. Qual. Assurance Res. Lab., Natl. Environ. Res. Cent. 298 p.

HORWITZ, W. (chairman and editor).
1965. Official methods of analysis of the Association of Official Agricultural Chemists. 10th ed. Association of Official Agricultural Chemists, Wash., D.C., xx + 957 p.

MOORE, W. A., R. C. KRONER, AND C. C. RUCHHOFT.
1949. Dichromate reflux method for determination of oxygen consumed. Anal. Chem. 21:953-957.

POJASEK, R. B.
1975. NPDES permits and water analyses. Environ. Sci. Technol. 9:320-324.

POPULATION BIOLOGY OF *EUPHAUSIA PACIFICA* OFF SOUTHERN CALIFORNIA

EDWARD BRINTON[1]

ABSTRACT

Euphausia pacifica was observed with respect to reproduction, growth and development of cohorts, and successions in population structure and biomass during 4 yr, 1953-56. The southern California eddy and its upwelling regime serve as a reproduction refuge for a warm-temperate population of this euphausiid. Three size classes spawn there during a year—the largest in April-June, an intermediate in June-February, and small, newly mature females usually in August-January. There were year-to-year differences.

The largest densities of larvae were observed about a month after egg peaks (one survey later) or appeared coincident with them. In 1953 there was strong spring recruitment, abruptly subsiding with an early decline in upwelling—the index of environmental enrichment used. During 1954 only one substantial cohort was recorded, in June at the height of a poor upwelling season. In 1955 repeated spawning occurred during the long upwelling season, but recruitment after July was poor. The year of most intense upwelling, 1956, yielded three strong cohorts—the last, July-October, being exceptionally strong. Smallest larvae were usually in 12°-16°C waters. Ripe females were concentrated at high densities at these same temperatures during August-March but were distributed over a broader range at 10.5°-19°C during April-July.

Growth was estimated to be about 3 mm body length per month, slowing during September-January or after about 17 mm. Females appeared to grow slower in breeding seasons. Maturity can be at 11 mm, but reproduction is not general until 15-16 mm. Here, maximum size was 21 mm after about 7 mo for early-year recruits and a year for summer recruits. Survival rates appeared higher in the latter. Growth rates were similar to those reported for *E. pacifica* off Oregon and higher than in the subarctic Pacific. Survivorship was lowest for furcilia larvae, increased in juvenile and young adult phases, then decreased after reproduction became regular. Slowed growth and increased survivorship at life interphases appeared to cause regular frequency and biomass maxima at lengths of 7, 10-12, and 15 mm. Sex ratio favored females. Males apparently accomplished multiple fertilizations.

Euphausia pacifica Hansen is a temperate North Pacific euphausiid crustacean, composing a substantial part of the zooplankton of the North Pacific Drift, lat. 40°-50°N, and ranging southward along the coast of North America as far as lat. 25°N (Brinton 1962a). In the cooler part of the California Current, it occurs in association with the euphausiids *Nematoscelis difficilis* and *Thysanoessa gregaria*. Depth ranges of the three species overlap daily as *E. pacifica* and *N. difficilis* engage in distinctive vertical migrations while *T. gregaria* does not migrate (Brinton 1967a). Horizontal ranges are sufficiently similar so that these species, together with *E. gibboides*, were considered the euphausiids of a California Current-Transition Zone plankton assemblage (Brinton 1962a).

Euphausia pacifica performs extensive vertical migrations. Off California it lives at daytime depths of 200-400 m, entering the surface layer at night. It is an omnivore (Lasker 1966) and possesses thoracic food-gathering limbs which are nearly uniform in length and in setation of the filtering screens.

Euphausia pacifica is usually the most abundant euphausiid. Its maximum densities are often centered relatively near to the coast of California. The low-latitude part of the population of *E. pacifica* is the object of this study. Aspects of its life history have been observed in the more typically temperate regime to the north of lat. 40°N (Nemoto 1957; Ponomareva 1963; Smiles and Pearcy 1971) where environmental characteristics show stronger seasonality than to the south. The extent to which the downstream portion of this distributional range is maintained by local processes has not been previously investigated.

The study was organized in relation to existing knowledge of the physical-chemical characteristics of the area and of the species distributions.

Surveys of the region of the California Current since 1949 have provided a reservoir of hydrographic data and plankton samples that lend

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themselves to time-series studies of biological and environmental developments. The CalCOFI (California Cooperative Oceanic Fisheries Investigations) Atlas series (Numbers 1-24) presented varied material, including euphausiid distributions derived from the program. Charts of distributions of *E. pacifica* based on the data that are the subject of the present analysis are included in Brinton and Wyllie (in press). Smith (1971) described the distribution of zooplankton biomass.

Description of the Study Area

The southern California eddy is the southernmost area in which *E. pacifica* is still both abundant (commonly 10-1,000 individuals beneath 1 m^2 of sea = 10-1,000 mg wet weight) and dominant among the larger zooplankters (Brinton 1967a, b). The eddy may be considered bounded on the north by Point Conception, lat. 34°N, and on the south by about lat. 30°N. Its east-west extent is about 250 km; beyond its western limits, flow is consistently from the north and apparently contributes relatively little water and biota to the eddy.

The sluggish circulation off southern California evidently permits substantial autonomy for the resident populations. The currents are commonly 5-10 cm/s and rarely as much as 25 cm/s, both at the surface and at 200 m depth (Wyllie 1966). Direction of flow sometimes reverses between these two levels. These are, respectively, the night and day depth levels occupied by vertically migrating *E. pacifica* (juvenile and adult) in the area; larvae remain near the surface day and night (Brinton 1967a).

Circulation of the eddy is cyclonic. Within it, therefore, there is upward transport of enriched water. The center of the eddy (no surface flow) is, on the average, near San Nicholas Island (lat. 33°15′N, long. 119°30′W), 100 km off the midpoint of the southern California coast. The study area was centered here. Farther east, mean flow is northwesterly along the coast. To the west, flow is southeasterly, angling toward the coast near lat. 30°N.

About 150 km south of Point Conception, mean geostrophic flow approaches 135°, averaging 10 cm/s. A parcel of water entering the eddy from the northwest would, at that speed, take 100 days to move around the eddy back to Point Conception, flow permitting. Average velocities within the eddy are much less. Places where substantial advection takes place across margins of the area are determinable from the flow diagrams in a relative sense. Northerly surface flow into and out of the area is characteristic of winter months when the Davidson Countercurrent is developed. Southerly flow into or through the western part of the area is usually strongest in April-July. The eddy persisted in almost all of the months studied.

Upwelling enhances the temperate character of the area during spring and summer, usually intensifying during April-June (Bakun 1973) when annual temperature minima are usually found. It is responsible for much of the local nutrient enrichment (Reid et al. 1958). Seasonal periodicity is evident when water temperature is averaged for the area of the eddy as a whole: August-October is generally warmest and January-April coolest (Anonymous 1963). The area contains a scatter of islands which provide substantial shoal grounds, regarded off Oregon to be areas best suited for *E. pacifica* (Smiles and Pearcy 1971). Such islands also provide topography for the formation of downstream eddies which are enrichment centers (Uda and Ishino 1958). They also serve as centers of upwelling. Here, upwelling is less dependent on the direction of the wind than on its intensity. However, the coast from Point Conception eastward remains the main focus of upwelling during the period of prevailing northwest winds, February-June. According to the indices derived by Bakun from extrapolated atmospheric pressure gradients at the sea surface, upwelling off southern California is the most intense to be found in the California Current.

For this initial life-history study, the period chosen (1953-56) was one of generally stable oceanic climate and hydrographic conditions, compared with the years immediately following, which included times of more extreme fluctuations in temperature and flow characteristics. During 2 of the 4 yr, 1955 and 1956, upwelling was inferred by Bakun (1973) to be more intense than the 1946-71 mean; however, during 1954 it was less, and during 1953 upwelling commenced early but barely achieved the June peak of mean intensity and was greatly diminished in the summer months.

Thus it was anticipated that the study period would yield observations of low annual variability in the population of *E. pacifica*, thereby providing a baseline against which eventually to measure events in years of known extremes in ocean climate, e.g., 1957-59 (Brinton 1960).

Previous Investigations

In addition to the observations on the life history of *E. pacifica* (Nemoto 1957; Ponomareva 1963; Smiles and Pearcy 1971), aspects of the energy budget and physiology of this species have been studied. Lasker (1964, 1966) measured moulting frequency, feeding rates, respiration and carbon utilization by specimens maintained in the laboratory, and observed growth rate in juveniles and adults. Fowler et al. (1971) considered effects of temperature and size on moulting. Small et al. (1966) measured respiration at different temperatures and discussed energy flow, while Small (1967) further examined energy flow. Paranjape (1967) made observations on moulting and respiration. Aspects of depth-habitat and pressure in relation to respiration were considered by Small and Hebard (1967), Pearcy and Small (1968), and Childress (1971). Gilfillan (1972) studied oxygen uptake in relation to laboratory controlled temperatures and salinities.

Total oocytes in a large female were counted by Ponomareva (1963). Clutch size estimates and the vertical distribution of different age groups were given in Brinton (1962b and 1967a, respectively).

Limitations of the Study

Understanding the population biology of an oceanic species depends in large part upon the extent to which a representative part of the population can be representatively sampled. In the planktonic environment, currents not only tend to transport the organisms across an observer's horizon, but also cause relative horizontal displacement of life stages because, in many species, the various stages of development live at different depths and experience different horizontal transport. This is true of euphausiids. Species undergoing both ontogenetic and daily vertical migrations, such as *E. pacifica*, are further subject to differential horizontal transport. Thus, water movement is a variable which complicates any plan for temporal continuity in sampling a population. The area covered and the time spent in carrying out an assessment of a population does not need to be great if the waters are restricted geographically and if growth and development of the population is measurable between successive assessments. Clearly, a gyre of circulation, such as the eddy lying off southern California, may be expected to harbor elements of a population that persists locally. This study area has proven practical in size according to the logistics of CalCOFI.

MATERIALS AND METHODS

Samples were obtained by oblique tows, 0-140 m depth (except where the water was shallower), using the CalCOFI standard net, 1-m mouth diameter and 0.55-mm mesh width (Ahlstrom 1948). The mesh width of the cod end and of a 40-cm section in front of it was 0.25 mm. The volume of water strained through a net was determined with a TSK (Tsurumi-Seiki Kosakusho) flowmeter.[2] Most volumes were in the range of 300-400 m^3. The net was towed at about 75 cm/s. The 1953-56 cruises provided month-to-month data, including more frequent surveys off southern California in late 1955 (four in September, three in November). Station positions and collecting data together with displacement volumes of the plankton samples are from annual listings of CalCOFI plankton sampling 1953-56 (South Pacific Fishery Investigations 1954, 1955, 1956; Thrailkill 1957).

Specimens smaller than 3 mm in length are able to pass through the meshes of the net and therefore were not representatively sampled. Smaller specimens (2 mm) are nevertheless retained by the fine meshes of the cod end of the net and counts of these are included as indicative of the presence of the small calyptopis larvae. Free floating eggs of *E. pacifica* are not retained by this net. Estimates of egg production are derived from examination of the ripe females sampled, as described in the discussion of fecundity below.

A total of 819 samples from 48 cruises, 5301 (January 1953) through 5612 (December 1956), were examined (Figure 4d). Only nighttime samples were used since juveniles and adults are not representatively sampled in the daytime, owing to vertical migration and avoidance of the net (Brinton 1967a). Between 7 and 43 nighttime samples were collected in the study area during each cruise. "Night" was considered to be the period from 1 h after sunset to 1 h before sunrise. A few sunrise and sunset samples were analysed if they were collected under overcast skies. A sample marginal to, but outside of, the area was studied when such a sample was from a locality nearer to the closest boundary of the area than any of the

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

sampled localities within the area. Thus, some samples from station lines 77 (northern) and 97 (southern), or designated 80.80 (western), were occasionally used.

The samples were examined in the following manner. An aliquot containing 100-200 *E. pacifica* was counted; the specimens were measured to the nearest millimeter of body length (tip of frontal plate to tip of telson); adults were sexed; and the degree to which the reproductive products were developed was recorded. If, for adults (specimens >10.5 mm in length), the initial aliquot contained fewer than three specimens of any particular length, a second aliquot of equal size was examined for specimens of that size or larger. In this way, increasingly large fractions of the sample were examined for specimens of those length intervals which were progressively determined to be fewest in the sample. This procedure made it possible to count the rarer, large specimens with a degree of accuracy comparable with that to which the consistently more abundant small specimens were counted. Usually, the entire sample was examined for specimens of more than 14-mm body length. This procedure was facilitated by the use of the Folsom plankton splitter which, through successive splitting operations, provides aliquots of ½, ¼, ⅛, ... $1/n$. All counts were standardized for 1,000 m^3 of water strained by the net.

After standardization, the counts for a sample (station) were weighted according to the proportion of the survey area represented by that station. When the nearest area surrounding the station was equal to a 65×65 km square (a usual spacing for CalCOFI stations), the weighting factor was 1.0. When areas represented by stations were greater or less than 65×65 km, weighting factors were proportionally greater or less than 1.0. The study area was equal to 19 65×65 km squares. Therefore the sum of the weighted abundances (for each size of *E. pacifica*) was divided by 19, providing a mean standardized abundance for the area for the given survey. (The night stations were not at the same localities on each cruise, though tracks followed by the vessels were generally repeated. Furthermore, as is to be expected, clusters of day stations tend to alternate with clusters of night stations. Unsampled parts of the area are expected to be better represented by samples from stations nearest to that unsampled part than by samples from more distant localities.)

Females were classified as 1) with ripe eggs (Mauchline's [1968] egg phase IV) and with attached spermatophore, 2) with ripe eggs and no spermatophore, 3) with ripening eggs (approx. Mauchline's phase II), or 4) ovary weakly developed. Adult males were categorized as 1) with ripe spermatophores, either protruding or internal, or 2) without ripe spermatophores.

Biomass was calculated using abundance at each body length (1-mm increment). Values are in terms of wet displacement volume (wet weight) of *E. pacifica*, given per body length increment in Miller (1966). The following conversion factors from Lasker (1966) may be applied:

Dry weight	= 17.2% of wet weight
Carbon	= 42 ± 1.7% of dry weight
Carbon	= 7.2% of wet weight

RESULTS

Southern California Eddy in Relation to the Rest of the California Current

October 1955 data (cruise 5510) illustrated characteristics of flow and temperature in the current, and occurrences of *E. pacifica* larvae (Figure 1a-c). These were general to fall-winter 1953-56 and placed the southern California area in broader geographical perspective. At that time the landward portion of the current, slow and cool, supported five centers of recruitment of *E. pacifica* (Figure 1c): 1) off San Francisco, probably related to the September peak off Oregon obsrved by Smiles and Pearcy (1971), 2) north of Point Conception, 3) southern California, 4) Point Colnett (lat. 31°N), and 5) Point Canoas (lat. 29°N). The three centers off California were then associated with current reversals while the two centers off Baja California were places where upwelling was conspicuous. A Punta Eugenia center, farther south (lat. 27°-28°N), usually supports *E. pacifica* earlier, during the local peak of spring coastal upwelling, May-June.

Direction and intensity of coastal flow tends to vary on a seasonal basis. During cruise 5510 and through ensuing fall and winter months, coastal currents off California provided means of northerly transport for portions of southern populations. During spring and summer, intensified southerly currents off northern California are expected to bring elements of the northern population into the southern California area via the offshore route west of Point Conception, diverting shoreward near lat. 32°N.

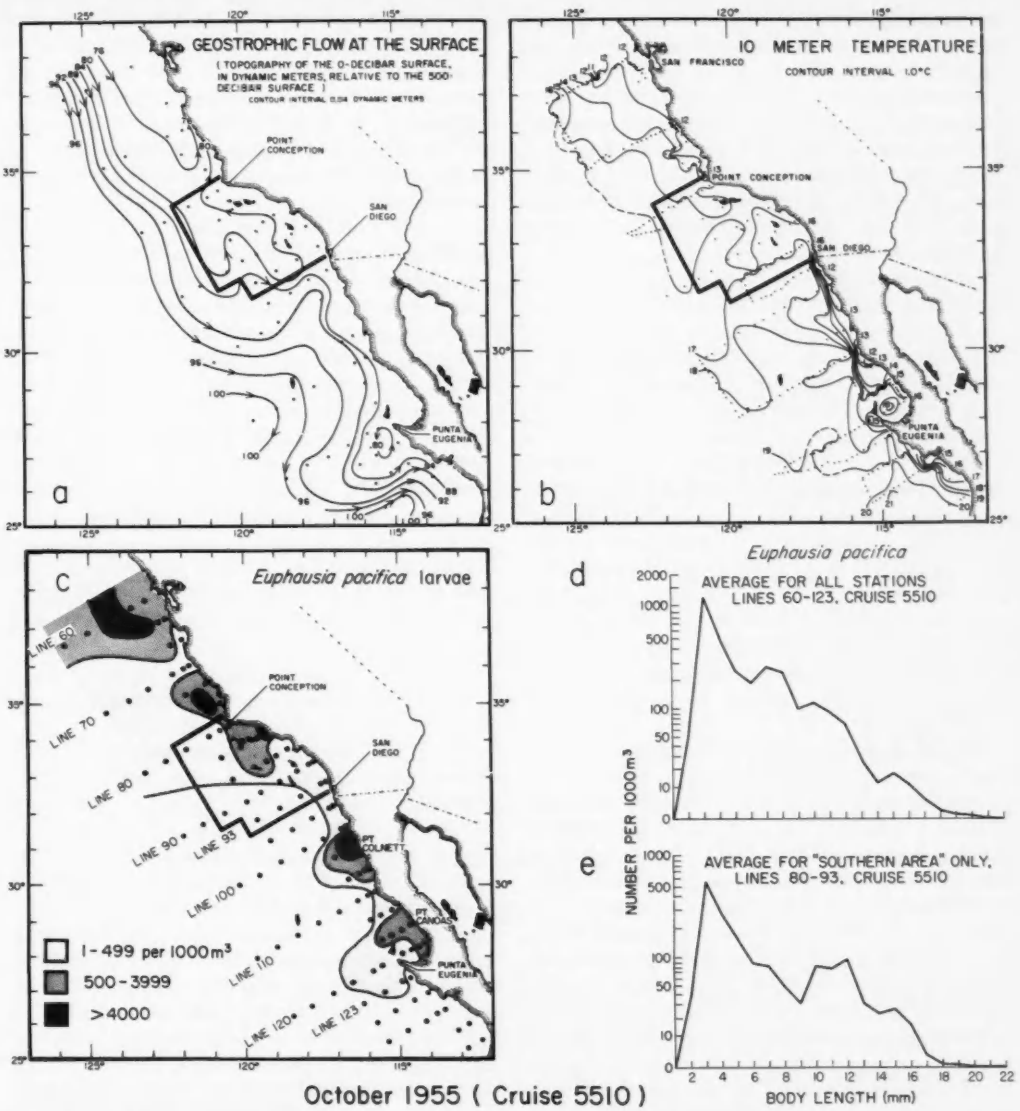

FIGURE 1.—October 1955 data (cruise 5510). **a**, Surface streamlines showing areas of current reversals off California and **b**, 10-m temperatures indicating upwelling centers along Baja California, both associated with **c**, aggregations of *Euphausia pacifica* larvae. Length-frequency distributions of *E. pacifica* are averages for **d**, all nighttime stations and **e**, stations within southern California area.

The length-frequency (L-F) diagram for *E. pacifica* in the California Current as a whole (cruise 5510) shows four modes present in the overall population: 3-4 mm (larvae), 7-8 mm, 10-12 mm, and 15-16 mm (Figure 1d). Time progressions in such modes are used below to estimate population development, including growth and mortality. The southern California part of the population is characterized by small (10-12 mm) and large adults (15-16 mm). It will be shown below that each of these two October 1955 modes is distinguishable within a month-to-month L-F sequence of cohort

development; the 10-12 mm group, most characteristic of the southern California area in Figure 1e, was of a cohort which remained locally dominant from its inception in July 1955 until January 1956.

The 7-8, 9-12, and 15-16 mm modes are described below as being common to *E. pacifica* because they are at body lengths at which life-phase changes and growth slows; therefore frequencies of those sizes increase, particularly during fall-winter periods of reduced food supply.

L-F curves for individual stations show the clear 7-8 mm mode along an "offshore" north-south track (Figure 2a, c) in the axis of the fastest part of the current (Figure 1a). It dominates the 9-10 mm mode as the transect, following the steamlines, angles shoreward along the southern edge of the southern California area, until lat. 35.5°N (station 97.50) where the 7-8 mm mode becomes inconspicuous and the 9-10 mm mode assumes dominance. Thus offshore, where southerly population transport would be expected on the basis of the observed current, dissipation of the L-F characteristic of the northern population takes place along the western limit of the study area. This is considered evidence that such transport then contributed little to the area's population, relative to more nearshore, local contributions.

Individual stations along a "nearshore" north-south transect (Figure 2b) showed a dense heterogeneous population of *E. pacifica* off San Francisco (station 63.55, lat. 37°N). Off central California (stations 70.55, 77.55), 7-8 mm juveniles became conspicuous (cf. Figure 3). Farther south, particularly in the southern California area (stations 83.51-90.28), 7-10 mm individuals were much reduced in numbers, while the frequency of the 11-12 mm size increased, appearing as a clear L-F mode. In October, larvae were few off northernmost Baja California where oceanic water typically moves eastware compressing shoreward the faunistic connection of the southern California area to more southern upwelling centers. To the south along the Mexican coast, the 11-12 mm mode characteristic of the study area reappeared, coincident with areas of production of larvae. Farthest south (off Punta Eugenia; stations 120.45, 123.40), modes were at 9-10 mm and at 3-mm larvae. These 9-10 mm specimens may be poorly nourished individuals, corresponding in age to 11-12 mm individuals occupying the area immediately to the north—an area which appears relatively fertile with respect to production of larvae. The same relationship was observed locally off northernmost Baja California; there the population having a 9-10 mm mode included few larvae (Figure 1c) and occupied an easterly incursion of oceanic water (Figure 1a), being bounded on the north and south by cooler and presumably more fertile areas in which both 11-12 mm and larval modes were again conspicuous.

At this time (October 1955) the range of *E. pacifica* terminated near Punta Eugenia, but it can extend to lat. 23°S (Brinton 1967b). These far downstream parts of the population appear reproductive, but to the south of southern California they are impermanent (Brinton 1967b, 1973). Mature or maturing individuals are expected to be intermittently injected from the north, particularly during the March-June period when southerly flow is intensified. These individuals may find local places of refuge in cool, slowly moving, productive coastal waters from Point Conception southward in association with upwelling centers. The southern California eddy is the largest such refuge, serving also as a major population center which has both coastal and oceanic dimensions.

Spawning and Recruitment

Spawning intensity was estimated indirectly since free-floating eggs were not sampled. Females bearing ripe eggs provided a means of estimating incipient spawning. All females having an attached spermatophore also carried ripe eggs in the ovary. From the several thousands of these counted, 373 of different body lengths were examined with respect to number of ripe eggs carried. The relationship between body length and mean number of ripe eggs was linear between 11 and 20 mm length (means were encompassed by 95% confidence limits of regression line), with the mean number of eggs extending from 20 to 212 across this range (Figure 3). Disproportionately small numbers of eggs were observed in the largest (>20 mm) females. Mean values for each body length were applied to the numbers of each length of ripe female counted in the plankton samples to estimate the spawning potential for each sampling period. These are underestimates since, for 60% of the surveys, the predicted values are not high enough to have produced the density of larvae found at the time of the next survey—even presuming only 50% mortality between surveys (Figure 4c). Evidently some eggs

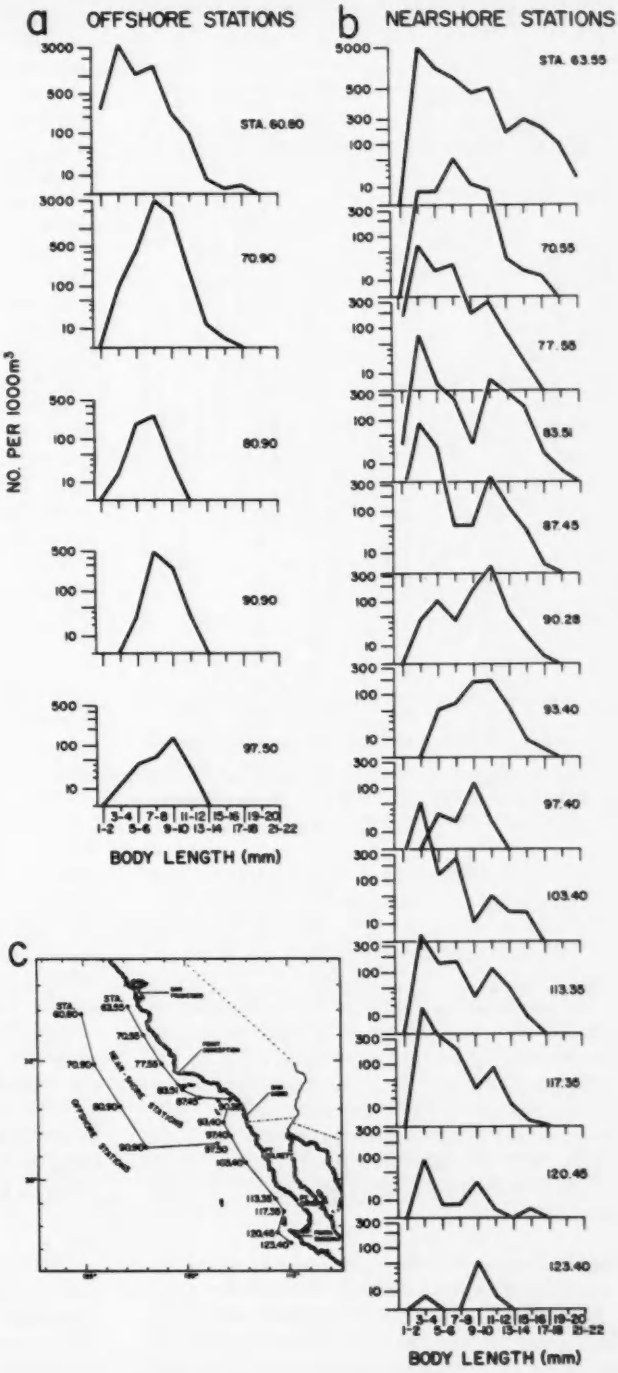

FIGURE 2.—Length-frequency distribution of *Euphausia pacifica* along north-south axes of California Current (cruise 5510). a, Approximately 250 km offshore; b, <100 km offshore; c, positions of stations.

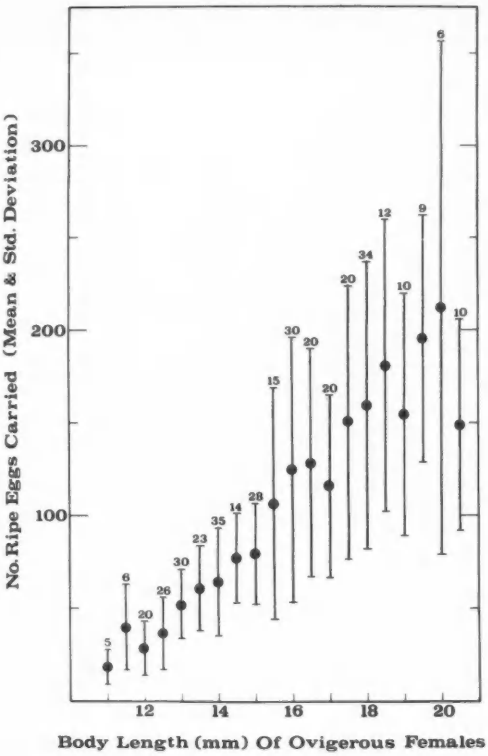

FIGURE 3.–Number of mature eggs in ripe spermatophore-bearing *Euphausia pacifica* in relation to body length. Numbers of individuals examined are indicated.

found to be immature at time of counting, either in ripe or other females, mature in time to contribute to the monthly spawn. The egg estimates are therefore regarded as only relative, month to month.

The production of eggs and larvae in each year (Figure 4c) was considered in relation to four parameters: 1) annual upwelling cycle in the southern California area inferred from atmospheric parameters (Figure 4a) and from minimum water temperatures (Figure 4b), 2) size structure of the spawning stock (Figure 4d), 3) zooplankton biomass (Figure 5a), and 4) *E. pacifica* biomass (Figure 5b).

1953

Upwelling began early (February, cruise 5302) with above-average intensity, accompanied by spawning in February and April. The February spawn, mainly by females of medium length (12.6-16.5 mm), led to discernable recruitment of larvae in March. The April spawn, mainly by large females (16.6-21.5 mm) led to the year's maximum recruitment in May-June. Upwelling peaked in June, and diminished to an unseasonably low intensity thereafter (Figure 4a), accompanied by local variability in water temperature through October (Figure 4b).

Substantial egg production during June-August, by medium-sized and small (10.6-12.5 mm) spawners, led to less recruitment than in April when spawning was of similar intensity. April was the start of the general spring zooplankton bloom (Figure 5a), presumably a response to the greater availability of phytoplankton food in the spring. Spawning diminished after August although larvae were evident in September and November. Small females became predominant after September when they became important contributors to the production of eggs.

These estimates of relative spawning are supported by a consistent relationship of egg peaks to larva peaks. Three of the four egg peaks in 1953 were followed by larva peaks a month later. Under conditions of laboratory hatching and rearing, euphausiids live as larvae for about 29 days (Gopalakrishnan 1973).

1954

Upwelling commenced in March (Figure 4a), a month later than in 1953. Local temperature minima, however, showed that this process was not obvious until April (Figure 4b). By both criteria, spring upwelling in 1954 was the least intense to be observed during 1953-56. (According to Bakun (1973), it was the least observed during 1953-71, though substantially greater than during 1947-52.) Production of eggs was initiated in March, evidently by a stock of large females derived from the September 1953 recruitment (see sections on growth and survival below, and Figure 9). Recruitment became intense only during June-July, associated with the one peak in spawning observed during 1954.

1955

As in 1954, upwelling started in March (following Bakun 1973, Figure 4a) or in April (using temperature minima, Figure 4b). There was a gradual increase in egg production begin-

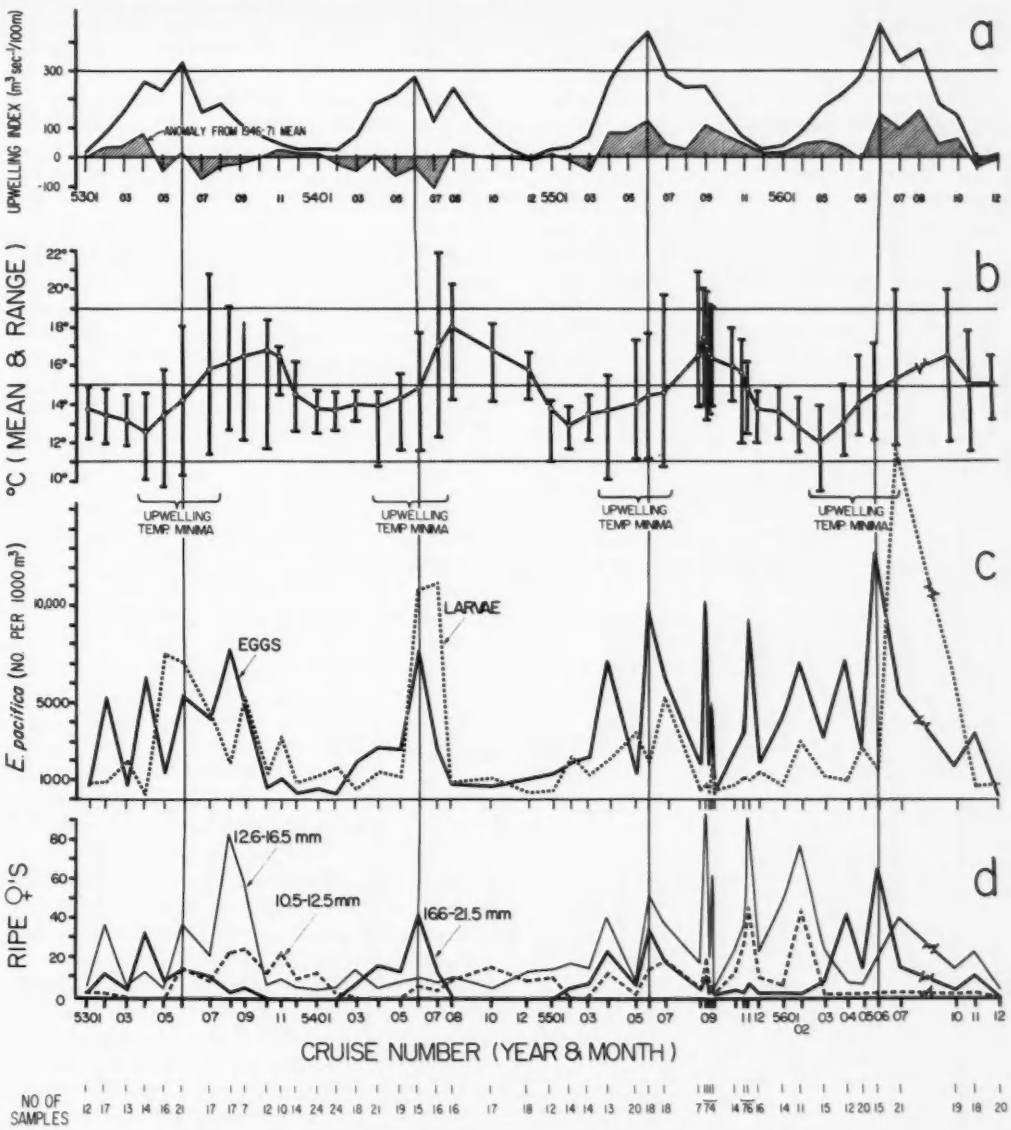

FIGURE 4.—**a**, Inferred monthly index of upwelling intensity per 100 m of southern California coastline, 1953-56 (from Bakun 1973). **b**, Temperature range and mean, by cruise, in study area. **c**, Estimated densities of ripe eggs and <4.5 mm larvae of *Euphausia pacifica* in area. **d**, Densities of ripe females, three body-length groups. Number of samples examined are indicated by cruise.

ning in December 1954, and the first significant recruitment was in February (cruise 5502). This increase in spawning continued through March, but recruitment did not increase markedly until May, following an April egg maximum. Thereafter egg production peaked in alternate months, June (the annual upwelling maximum), September, and November—but recruitment was generally low (<2,500 larvae/1,000 m³ in the area) except during May and July. July yielded the year's peak in

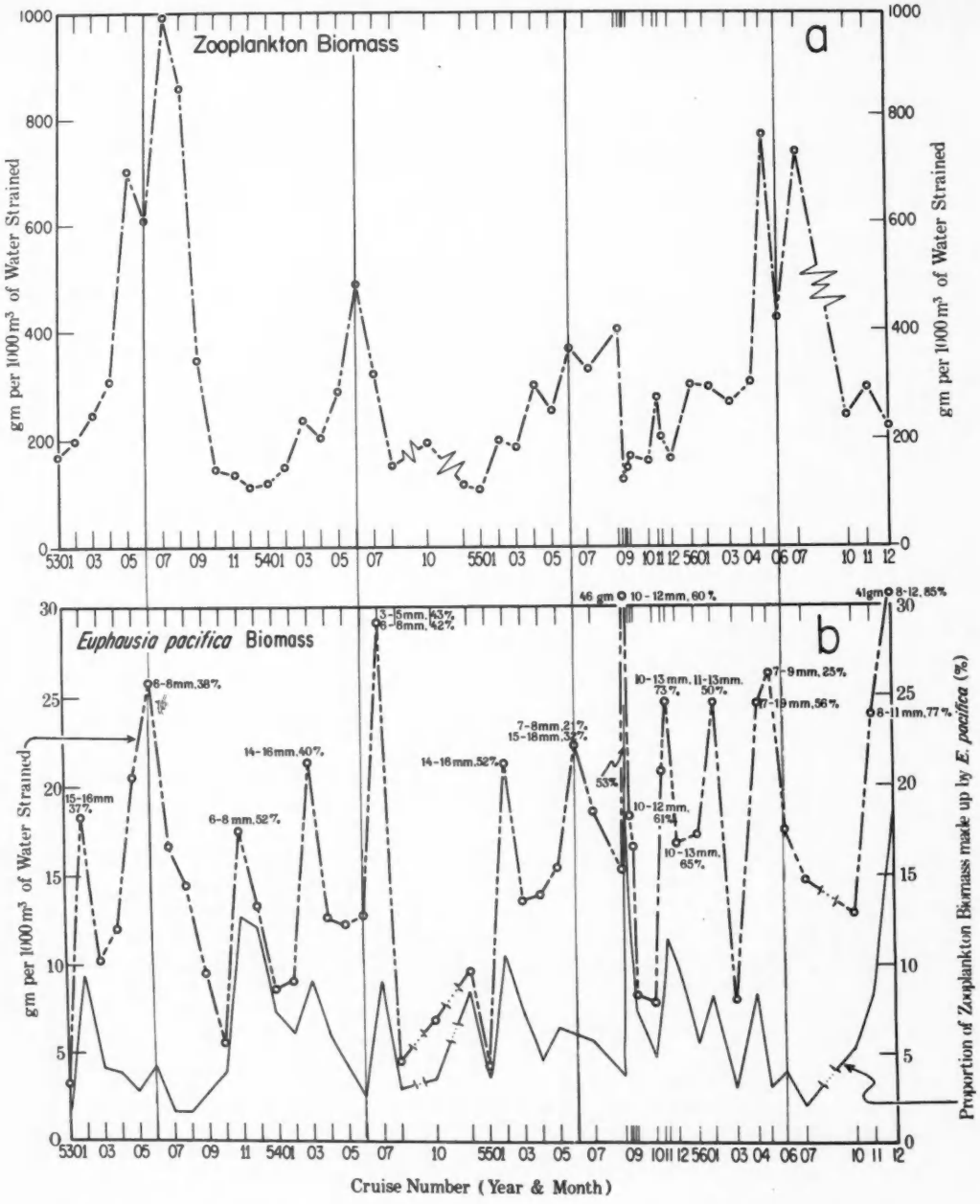

FIGURE 5.—Mean biomass, by cruise, of a, zooplankton in southern California area, based on same samples examined for euphausiids; and b, biomass of *Euphausia pacifica* and its proportion of zooplankton biomass, with dominant body lengths indicated.

larvae. Large and medium-sized spawners were substantial contributors to this recruitment. The latter were predominant and continued to be throughout 1955. This differed from 1953, 1954, and 1956 when small or large spawners were predominant during at least part of the year.

In September a brief increase in larvae closely followed the year's peak in potential egg production, as observed during four September cruises closely spaced in time. This was at the time of maximum water temperatures (Figure 4b). The November peak in eggs, to which small spawning females contributed importantly for the only time in 1955, led to a slight increase in recruitment in December. This November activity was associated with residual upwelling that was significantly more intense than the 20-yr November mean.

1956

Upwelling began early in February as in 1953. February spawning was also high, as in 1953 and differing from 1954-55. Spawners were small and medium-sized females (Figure 4d). Larvae peaked during the same month. Following a March decline in eggs and larvae, April spawning returned to the February level associated with the usual spring appearance of large spawners. This egg maximum was followed in May by a small peak in larvae. In June, egg production reached a peak for the 4-yr period (13,000 eggs/1,000 m^3) at the same time as a 4-yr peak in the upwelling index which, however, was not confirmed by the observed temperature minima (Figure 4a, b). In July 1956, larvae showed strong survival from the June spawn with a density of 17,000/1,000 m^3. While the upwelling index continued to be well above average through August, CalCOFI sampling did not resume until October. Therefore, August-September recruitment was not recorded. High numbers of larvae observed from 28 September to 5 October (5,000/1,000 m^3) together with record numbers of 8-11 mm juveniles appearing in November-December (Figure 10) indicated that August-September spawning was heavy and greater than the substantial August-September spawn of 1953.

An increase in egg production in November 1956 resulted in little recruitment in December, after upwelling had stopped. An explanation may be inferred from the fact that, though zooplankton biomass had peaked earlier (May-July, 5505-07), the euphausiid part of the biomass became extremely high (24-41 g/1,000 m^3) only in November-December, consisting largely of 8-12 mm juveniles and young adults (Figure 5b). *Euphausia pacifica* then made up a larger proportion than ever before of the total biomass (15-20%), indicating a diminished amount of organisms of other taxa, such as salps and copepods. These, like larval euphausiids, depend heavily upon primary production for food. Their reduced numbers suggest diminished phytoplankton food (unless their mortality was not food related), hence the poor December survival of *E. pacifica* larvae emerging from the November spawn. Additional evidence of diminished food in November-December will be seen in the negligible rate of growth during November-December of the massive population of 8-12 mm *E. pacifica*. Alternatively, this population may have consumed the November larvae as well as their food, but this presumption is not supported by its low growth rate.

Recruitment Efficiency and Spatial Aggregation of Eggs

The relationship of spawning potential (density of ripe eggs) to larvae subsequently recruited is irregular, although a trend (Figure 6) indicated that efficiency of recruitment from available eggs was better during spring and summer (March-September) than during fall and winter (October-February). In 1953 the spring-summer peaks in

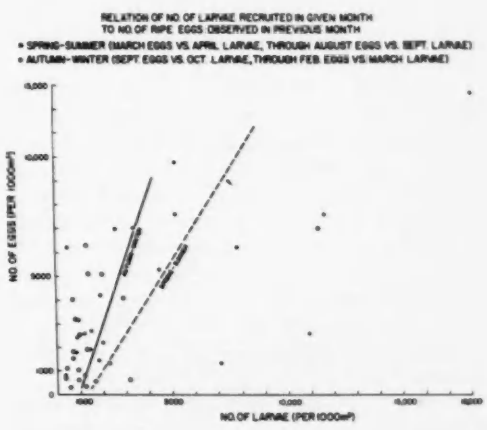
RELATION OF NO. OF LARVAE RECRUITED IN GIVEN MONTH
TO NO. OF RIPE EGGS OBSERVED IN PREVIOUS MONTH
• SPRING-SUMMER (MARCH EGGS VS. APRIL LARVAE, THROUGH AUGUST EGGS VS. SEPT. LARVAE)
◦ AUTUMN-WINTER (SEPT. EGGS VS. OCT. LARVAE, THROUGH FEB. EGGS VS. MARCH LARVAE)
NO. OF EGGS (PER 1000m³)
NO. OF LARVAE (PER 1000m³)

FIGURE 6.—Density of <4.5 mm *Euphausia pacifica* larvae in given month in relation to ripe unspawned eggs observed previous month, 1953-56 data. Regressions (Bartlett's test) for spring-summer (March-September) and autumn-winter (October-February) data are not significantly different.

egg production were followed by proportionately high peaks in larvae, relative to 1955 and early 1956 (January-April) (Figure 4c). Both the one peak in eggs in 1954 (June) and the highest peak in 1956 (June) led to particularly heavy recruitment.

Incipient spawners and larvae were both unevenly distributed in the study area, the larvae usually more patchy than the spawners (Brinton and Wyllie in press). A possible effect of relative aggregation of spawners on recruitment was considered. A monthly index of survival of newly hatched larvae was determined as the ratio of the mean density of larvae observed on a given cruise to the density of ripe eggs calculated for the previous month—usually one cruise earlier. (As noted above, this ratio is >1.0 in about one-third of the instances, indicating that spawning is underestimated. The indices are, therefore, regarded only as relative to each other.) Cruise-to-cruise differences in patchiness of spawners were estimated by comparing, among cruises, variances of number of ripe eggs carried by incipient spawners. Each variance was derived by use of numbers from all stations of a cruise. The regression of patchiness in relation to survival of calyptopis larvae showed a slope not significantly different from zero (Figure 7). Evidently, differences in the degree of aggregation of spawners on the scale observed (32-64 km between stations) did not affect survival of newly hatched larvae.

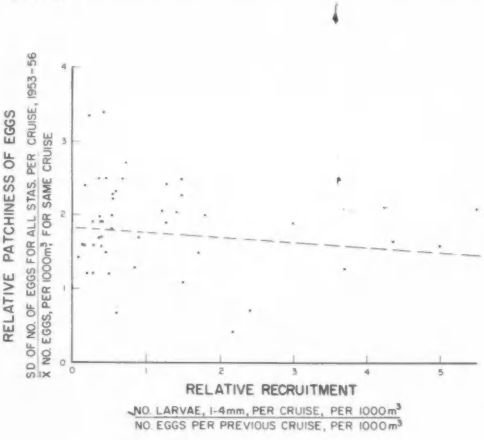
RELATIVE PATCHINESS OF EGGS
S.D. OF NO. OF EGGS FOR ALL STAS. PER CRUISE, 1953-56
X NO. EGGS, PER 100Om³ FOR SAME CRUISE
RELATIVE RECRUITMENT
NO. LARVAE, 1-4mm, PER CRUISE, PER 1000m³
NO. EGGS PER PREVIOUS CRUISE, PER 1000m³

FIGURE 7.—Index of patchiness of ripe unspawned eggs of *Euphausia pacifica* in relation to index of recruitment during succeeding month. Slope of regression not significantly different from 0 ($P>0.05$, t-test). Standard deviation is used as a measure of dispersion and in no way assumes normality of the data.

Temperature Relationships of Spawners and Larvae

Abundances of spawners and recently hatched larvae (calyptopes of <2.5 mm) were plotted in relation to ambient temperature at 10 m depth (Figure 8). A relationship of spring-summer upwelling to maxima in reproduction, however indirect, was evident in foregoing observations. Therefore, data for the months of strong upwelling (April-July) are separated from those of the other months.

Both spawners and larvae occurred across a range 10°-21.6°C, virtually the available range. When lumped by 0.5°C increments, close to 40% of the stations yielded some calyptopis larvae and 40% yielded incipient spawners. During August-March (Figure 10a) larvae were most concentrated within the range of 12°-16.5°C, the same as the spawners. There, mean densities of larvae were 50-200/1,000 m³. During April-July (Figure 8b), maximum densities of larvae, 200-7,000/1,000 m³,

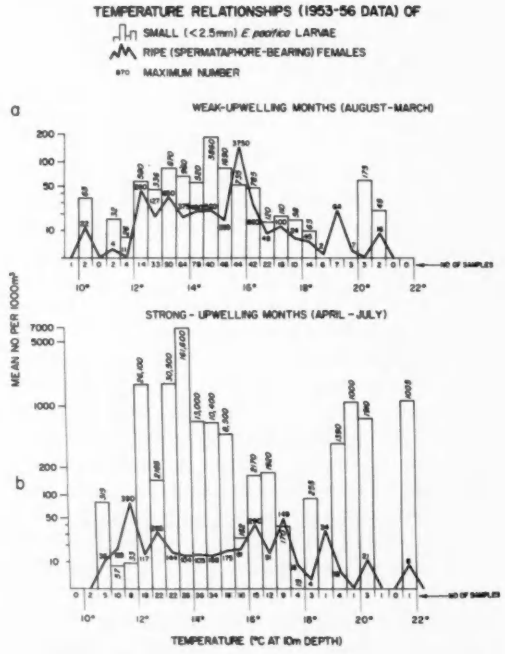

FIGURE 8.—Densities of *Euphausia pacifica* larvae <2.5 mm length and ripe females in relation to water temperature at 10 m depth. a, August-March; b, April-July.

were within a somewhat narrow range of temperature, 12°-15.5°C, as compared with the weak-upwelling period, and most spawners were within a broader range, 11.5°-17.5°C.

By years, during 1953, 1955, and 1956 the mean maxima of larvae were at 14°-15°C. In 1954 there were maxima at both 13°-14°C and 14.5°-16°C. Occurrences of larvae and spawners at temperatures >18.5°C during January-March and August-December were only during 1955, the year in which spawning extended on into September and November. Occurrences of April-July larvae at temperatures >18°C were all during 1954, the year of weakest upwelling, except for a single record in 1953.

Overall frequency of spawners did not differ between the periods of strong and weak upwelling, in contrast to large differences in the frequency of recruits. This implies that factors other than temperature are important to recruitment—probably the production of food associated with the upwelling period. Patchy local increases in surface nutrients associated with the upwelling season of 1969 are described in the Discussion.

It is also noteworthy that during periods of both strong and weak upwelling, mean maxima of spawners occurred at or just outside the limits of the optimal temperature range for recruits: during weak upwelling months, at 12°-12.5°C and 15.5°-16°C; and during strong upwelling months, at 11.5°-12°C and 17°-17.5°C. This implies that stations showing maximum densities of larvae and those showing maxima of spawners were mutually exclusive—an impression gained earlier during counting. Removal of adults from the region where they might fortuitously feed upon their young could be brought about by the vertical migration of the adults and their consequent differential transport at greater daytime depths, in accordance with the hypothesis of Hardy (1956).

Growth

Monthly L-F polygons for *E. pacifica* consistently peak at larvae 3-4 mm in length (Figures 9, 10). In the stream of continuous recruitment, a month-class is first distinguishable as high numbers of larvae relative to those produced in the months before and after. Subsequent growth can be traced through successive months as an L-F mode, either in the form of a crest, irregularity in slope, or change in height relative to the month before. Observations of growth and survival appear most reliable when cohorts are traced that begin as densities in excess of 2,000 larvae per 1 mm length increment per 1,000 m^3.

A cohort is designated by the year-month (e.g., 5303) in which its larva maximum is observed. Presumed relationships of egg maxima (Figure 4c) to subsequent recruitment are indicated in Figure 12.

When presented in terms of biomass (Figures 9, 10), population composition differs from that indicated by length frequency. For example, biomass modes may increase in height with time owing to growth, while corresponding L-F modes decrease in height because of mortality. As a consequence, cohorts are often more conspicuous when plotted as biomass. Biomass is plotted on a linear scale while abundances (length frequency) were plotted on a logarithmic scale to accommodate fluctuations in the many larvae and the few large adults. The biomass of larvae was generally low but periods of heavy recruitment are conspicuous.

1953 Cohorts

A small February 1953 cohort (Figures 9, 12) was tentatively traced through April as 10-11 mm adolescents. More substantial recruitment occurred in March from the February egg maximum, followed by little recruitment in April; growth appears to have been to 7-8 mm in April, 10 mm in May, 13 mm in June, 15-17 mm in July, 18 mm in August, and 18-19 mm in September.

Production of larvae first became intense during May-July 1953 (cuises 5305-5307), resulting in a broad mode recognizable as 3-7 mm in June (enclosed by a pair of dashed lines in Figure 11, one originating at 3 mm in May and the other at 3 mm in June). July larvae appeared to show poor survival, as shown in the reduced 5-7 mm component of the population in August. This is interpreted as leading to graphic separation of the May-June cohort as a conspicuous L-F mode, first observed in August (5308) as 8-13 mm juveniles and young adults (Figures 9, 11a), persisting into September at 12-15 mm, and perhaps surviving without growth into October, though decimated. Development of this cohort is even more conspicuous through the sequence of biomass modes.

An increase in recruitment in September (5309) over August, followed by low production in October, yielded a particularly conspicuous cohort

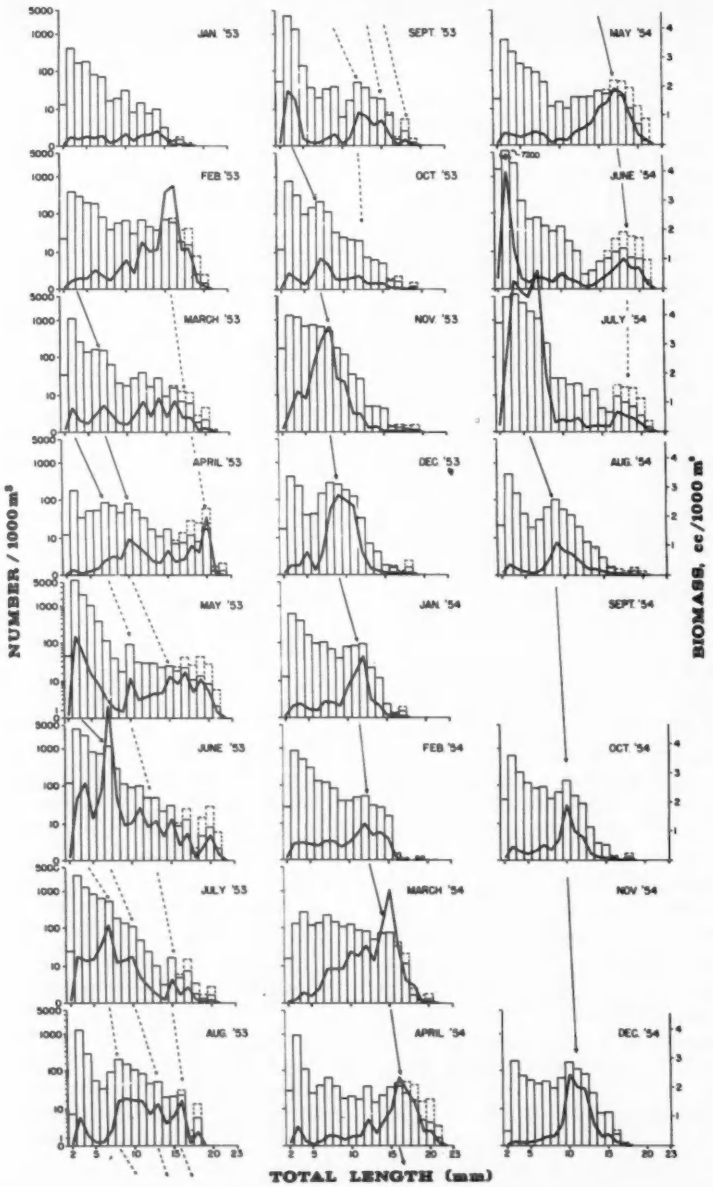

FIGURE 9.—Length-frequency (histograms) and biomass (line graphs) distributions, of *Euphausia pacifica*, 1953-54 cruises. Dotted boxes appended to histograms for body lengths 16-21 mm are corrections for net avoidance using Isaacs' (1965) factors derived for anchovy larvae of those sizes. Corrections are not applied to biomass. Arrows trace development of cohorts. Solid arrows trace sequences considered clear, dashed arrows trace those less clear.

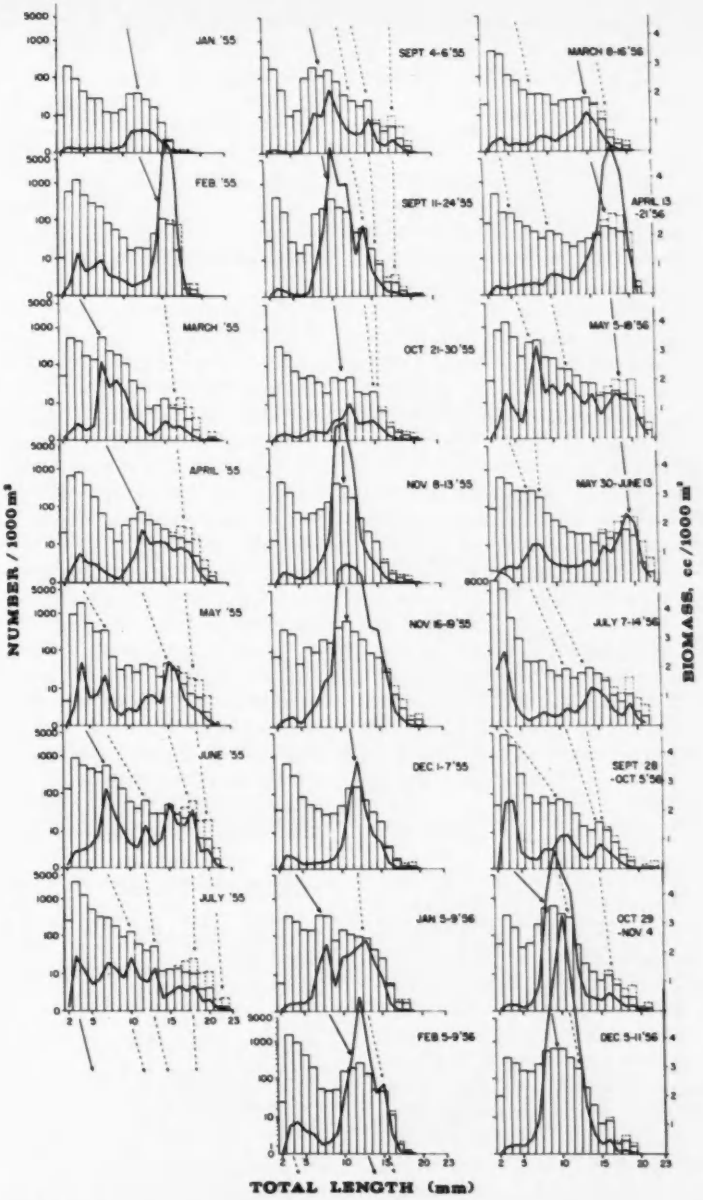

FIGURE 10.—Length-frequency (histograms) and biomass (line graphs) distributions, of *Euphausia pacifica*, 1955-56 cruises. Dotted boxes appended to histograms for body lengths 16-21 mm are corrections for net avoidance using Isaacs' (1965) factors derived for anchovy larvae of those sizes. Corrections are not applied to biomass. Arrows trace development of cohorts. Solid arrows trace sequences considered clear, dashed arrows trace those less clear.

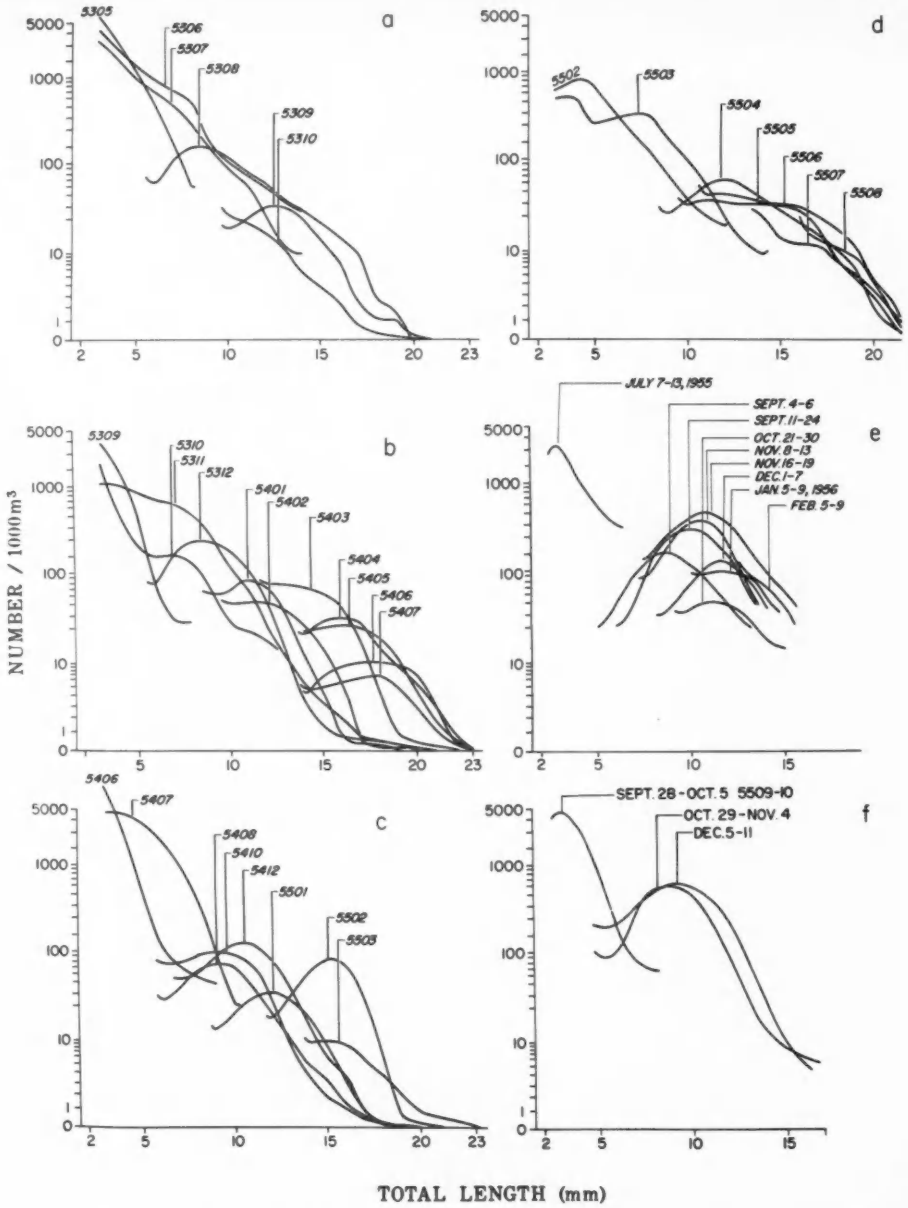

FIGURE 11.—Cohort development of *Euphausia pacifica*, shown as progressions of length-frequency modes. Curves are three-point running averages of portions of histograms in Figures 9 and 10. Cohort is identified by date (cruise) at appearance of conspicuous mode of 2-3 mm larvae. **a**, 5305; **b**, 5309; **c**, 5406; **d**, 5502; **e**, 5505; **f**, 5509-10.

traceable for 10 mo through July 1954 (5407) when it had achieved large-adult size, 17-20 mm (Figures 9, 11b, 12). Separate L-F curves for males and females (Figure 13), commencing at the onset of maturity ca. 11 mm, show that the modes for the 5309 cohort illustrated in Figures 9 and 11b actually are made up of paired overlapping peaks, for females regularly at a larger body-length increment by about 1 mm and for males where the difference in absolute frequency between males and females is greatest.

It is not likely that females, upon maturity, have undergone sudden, relatively rapid growth so as to exceed males in size. The curves (Figure 13) show larger females to be at a relatively greater frequency than males and the converse would be expected with increased female growth-rate. (Average male/female ratio is probably 1:1 at onset of adulthood, discussed under Sex Ratio.) Rather, the most mature females—those at the leading edge of the mode-cohort at the onset of February-March breeding—are growing slower than before, thereby appearing more numerous. At the same time, decreasing relative male survivorship could contribute to the increasing inequality in sex ratio. At body lengths >16 mm, females tend to dominate by 2:1 or more, indicating that they then spend twice as long as males at given sizes, at least while breeding, or that their survivorship is then greater, or that males remain below sampling depths at night. These alternatives are considered in the discussion of Sex Ratio, below.

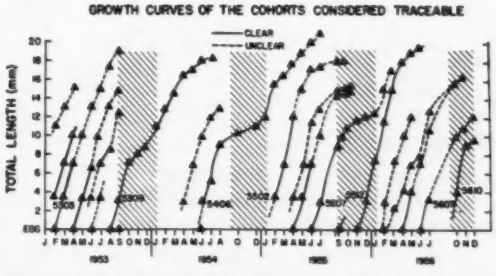
GROWTH CURVES OF THE COHORTS CONSIDERED TRACEABLE
CLEAR
UNCLEAR
TOTAL LENGTH (mm)
5308
5309
5406
5407
5410
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J S O N D J F M A M J J O N D
1953
1954
1955
1956

FIGURE 12.—Growth curves of *Euphausia pacifica* inferred from length-frequency modes. Clear (solid lines) and unclear (dashed lines) sequences as in Figures 9 and 10. Times of egg production are extrapolated, see Figure 4c. Fall-winter period of slowed growth is crosshatched.

1954 Cohorts

The single intense spawn of 1954 (June) led to strong June-July recruitment, establishing a cohort (5406) that was followed through a 10-mo period to 17-19 mm in April 1955 and, with less certainty, to 20 mm in June (Figures 9, 10, 11c, 13).

1955 Cohorts

Conspicuous 1955 cohorts arose in February (5502) and July (5507). The former appeared to attain 18 mm after 7 mo (September) and the latter reached 17-18 mm after 8 mo, following slowed growth during October-January (Figures 11d-e, 12). This cohort appeared at too-low density in October (5510) relative to a month later. This may be due either to sampling variability or to "piling up" at the 11-12 mm increment in November owing to growth being faster into the newly adult phase than out of it, energy then being diverted to gonad development. Nevertheless, it is noteworthy that the 5502 and 5507 cohorts appeared to be distinguishable in October (5510) as modes of 10-12 mm and 15-16 mm, Figure 1e, discussed earlier when the southern California area was compared with the California Current as a whole.

The December 1955 cohort was the only distinct year-end cohort observed during 1953-56 (Figures 10, 12, 13). It grew rapidly at 4 to 5 mm/mo during December-February and 3 to 4 mm/mo during February-April, apparently attaining 18 to 20 mm length by June 1956.

1956 Cohorts

These were scarcely traceable except for that appearing as 8-11 mm individuals in early November and as 8-12 mm in December. This mode doubtless derives from extremely dense larvae sampled during 5507 and 5509-10, its crest appearing to relate mainly to the latter. The small biomass peak at 10-11 mm during 29 September-5 October is clearly derived from the very heavy July recruitment. It subsequently becomes indistinguishable during November and December from the biomass of 8-12 mm juvenile-adults considered to have grown from 5509-10 larvae. The 29 October -4 November peak appears most likely to have derived from the 5509-10 larvae.

Survivorship

The average L-F distribution for all samples (Figure 14) shows that decline in density with body length is roughly exponential. The decline is

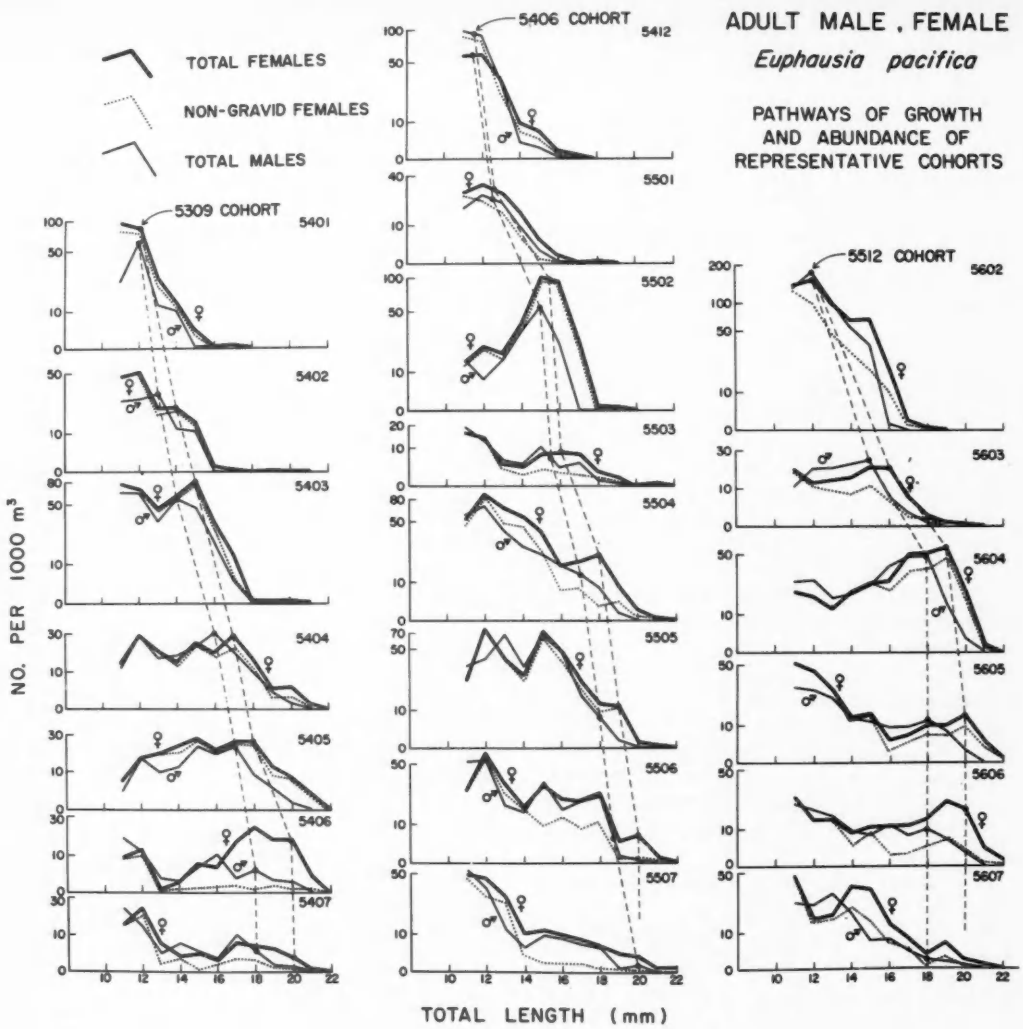

FIGURE 13.–Length-frequencies of adult males and females of *Euphausia pacifica*. Dashed lines trace development in males and females. Frequencies of females without ripe eggs are indicated (pertinent to discussion of Sex Ratio).

rapid during the larval phase and slower thereafter until large adulthood, 18-19 mm. Positive perturbations appear at 6-7 mm, 9-10 mm, and 14-15 mm. Average survivorship is 16% during the 1 mo furcilia larva phase, as seen in the decline in mean population density from 1,850 to 300/1,000 m^3 (Figure 14) between 3 mm and about 6 mm in body length which Boden (1950) has shown to be larval phase. For juveniles, 6 mm through 9 mm, survivorship is near 67%/mo over about 2 mo.

For adolescents and young adults of 9-14 mm, average survivorship remains nearly the same, 64%/mo, then decreasing to 60%/mo through 18 mm. After that, population decline appears rapid, possibly because sampling of such large individuals is not representative. Apparent

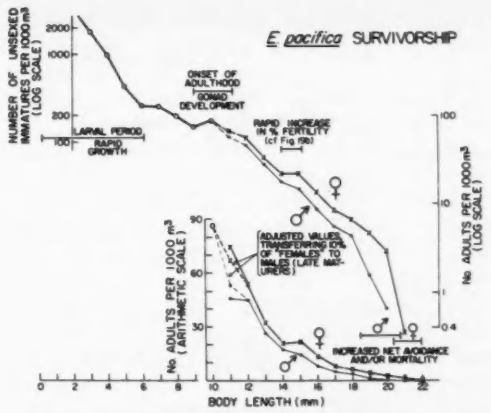
E. pacifica SURVIVORSHIP
NUMBER OF UNSEXED IMMATURES PER 1000 m³ (LOG SCALE)
ONSET OF ADULTHOOD GONAD DEVELOPMENT
LARVAL PERIOD
RAPID GROWTH
RAPID INCREASE IN % FERTILITY
ADJUSTED VALUES, TRANSFERRING EVIL OF "FEMALES" TO MALES (LATE MATURES)
No ADULTS PER 1000 m³ (ARITHMETIC SCALE)
No ADULTS PER 1000 m³ (LOG SCALE)
INCREASED NET AVOIDANCE AND/OR MORTALITY
BODY LENGTH (mm)

FIGURE 14.—Catch curves for all *Euphausia pacifica* sampled, densities shown on logarithmic and linear (adults only) scales. Periods of changing slope (changing survivorship, net avoidance and/or growth rates) indicated as related to life phases. Scale used for density of sexed adults (right) is doubled for lumped immatures (left).

differences in survivorship between males and females (Figure 14) are discussed below under Sex Ratio.

Survival rates for individual cohorts were approximated from relative amplitudes of month-to-month modes in the sequences used to trace growth (e.g., Figure 11). Percent survivorship plotted against estimated age shows cohort curves to be similar (Figure 15a). A positive change in slope consistently occurs within the range of 8-12 mm body length encompassing adolescence. However, regressions of $\log_{10}$ density on age take two forms:

1) Mean life-span survival rate calculated as a single linear regression for individual cohorts is highest among those recruited during June-December (06-12). For example, it is 51%/mo for the 5512 cohort, 58% for 5610, and 59% for 5309. In such late-year cohorts most of the juvenile-adult phase is during August-March, the period of reduced food and slowed growth. For example, the cohort 5507 attained adolescence (9-10 mm) in September and large adulthood (17 mm) in March (Figure 15b), having an estimated life span of 10 mo. (Egg stage to 3 or 4 mm length is considered the first month.) The cohort 5406 (Figure 15c) attained adolescence at 9 mm in August, appeared to show strong survival through 15-16 mm in February, and was distinguishable at 20 mm size in June—a life span of 13 mo. Thus those cohorts which attained 15-16 mm with densities >50/1,000

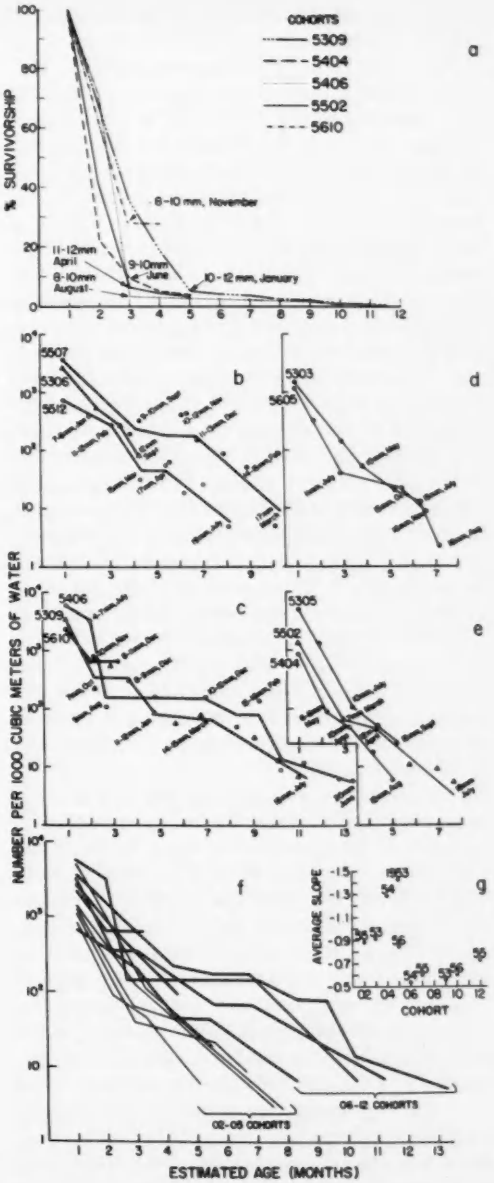

FIGURE 15.—Survivorship of cohorts of *Euphausia pacifica*, from amplitudes of length-frequency modes. a, Percent survivorship showing rapid decline until adolescence, ca. 9-11 mm. b, c, Age-frequency distributions of 06-12 cohorts smoothed for apparent piling up at times of slowed growth. d, e, Age-frequency distributions of 02-05 cohorts. f, Curves seen in b-e, clustered. g, Average slopes (from straight line regressions) for 02-05 cohorts seen as steeper than for 06-12 cohorts.

m^3 by February-March continued to be evident on into the spring bloom.

Two exceptionally large cohorts, 5406 and 5507, were initiated during late June-July. At first, these survived poorly, 8-10%/mo for 5406 through August-September and 40%/mo for 5507 through October (Figures 11c, f; 15b, c). Growth apparently then stopped after 9-11 mm body length, and the density had declined to 100/1,000 m^3. This took place when the onset of maturity was in September-October. This is presumably the start of the fall-winter period during which food supply is inadequate to permit both gonad development and size increase. During October-December, the 10-12 mm sizes increased in frequency, indicating continuing growth into that range by younger elements of the overall population and much reduced growth out of it. Therefore survivorship of the 5406 and 5507 cohorts during September-December could not be determined, but it appears to have been high. By January, body-length growth of these cohorts, now numerically enhanced, resumed. Survivorship of "5406" prevailed at about 47%/mo through June 1955 (21 mm), and for "5507" at 40%/mo as before September.

The large 5607 and 5610 cohorts appear to have undegone similar development (Figure 10), appearing to coalesce at 9-12 mm during November-December, with much increased frequencies at those body lengths.

2) Survival rate is poorer, 26-45%/mo, for recruits produced earlier in the year, February-June. Mean life-span survival was 43%/mo for the 5303 cohort, 26% for 5305, 37% for 5306, 30% for 5404, 44% for 5502, and 45% for 5605. Nonlinear details of survivorship in these cohorts are depicted in Figure 15d, e, while differences between early-year and late-year cohorts in mean slope of survivorship regressions are seen in Figure 15g. Coincidence of the juvenile-adult phases of early-year cohorts with the productive period May-September evidently accounts for the observed rapid growth during this period, hence the poor survival rate. These cohorts were traced to body lengths of 16-18 mm after 7.5-8 mo (5502, 5303, 5605) or to 13-15 mm after 4-5 mo (5404, 5305). Having declined to densities <10/1,000 m^3 during summer-fall, they were no longer recognizable in winter sampling.

Annual Biomass

Annual biomass by body length shows year-to-year similarities (Figure 16). Peaks are at 1) 3-4 mm, owing to consistent abundances of larvae in early furcilia phase; 2) 7 mm (except 1956), the onset of juvenile phase; 3) 10-12 mm (9-11 mm in 1956) the onset of adult phase; and 4) 15 mm, early in the peak reproductive phase. It was noted (Figure 5b) that monthly biomass peaks were usually dominated by one or another of these four body lengths. The larva peak occurs in spite of rapid early growth. The other three peaks are at ages when slowed body-length growth would be

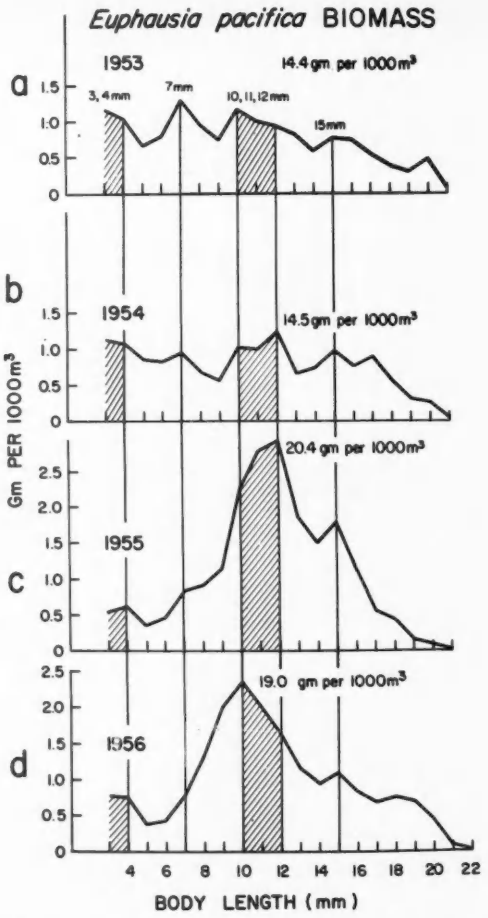

FIGURE 16.—Biomass, annual mean values for *Euphausia pacifica* and distributions per 1 mm body length. **a, b,** Uniform distributions for 1953, 1954, with modes at 3-4 mm, 7 mm (onset of juvenile phase), 10-12 mm (onset of adulthood) and 15-16 mm (start of maximum egg production, cf. Figure 21b). **c, d,** Distributions, strongly peaked at adolescence, biased by large 5507 and 5609-10 cohorts respectively.

expected: onset of juvenile phase, onset of gonad development, and time of maximum gamete production.

Biomass on body-length distribution was most even during 1953 and 1954 (Figure 16a, b). Recruitment in May and September 1953 led to the 7-mm peak of that year, and the September cohort was the main contributor to the 10-12 mm peak. The 1954 crest at 10-12 mm stemmed mainly from October and December sampling of the June 1954 cohort.

In 1955 and 1956, 3-4 mm larvae were reduced in average biomass compared with 1953 and 1954 while biomass of 9-12 mm adolescents was two times greater. The November 1955 stock of 11-12 mm stages (5507 cohort) was mainly responsible for the 1955 biomass peaks. The November-December 1956 stock of 9-11 mm stages (5609-10 cohort) provided much of the 1956 peak.

Large 18-20 mm adults showed their greatest biomass in 1956 following the strong upwelling year 1955, and lowest in 1955 following least productive year 1954.

Monthly changes in biomass are traced for each of three conspicuous sizes (Figure 17). Small (7 mm) juvenile bulk is greatest within May-July following spring recruitment. Other high values for the 7-mm size are not consistent seasonally, occurring during October-March.

Adolescents (10 mm), considered representative of the 9-12 mm juvenile-adult phase change, tend to be at greatest volume during August-January (when the smallest spawners, 10.6-12.5 mm, were also observed to peak, Figure 4d). Increased survivorship and slowed growth during fall-winter maturation of spring cohorts, discussed above, are considered responsible.

Subsequent February-March peaking of biomass at 15-mm size occurs as egg development accelerates. (This is preliminary to the appearance of the large >16.5 mm spawners during April-June, Figure 4d.)

A close relationship is evident (Figure 17) between biomass of each of the three sizes and their percent of the total *E. pacifica* biomass. This indicates that a given month's increase in biomass of the 7-mm size (or of the 10-mm or 15-mm size) is not accompanied by proportionate increase in the composite biomass of all other sizes. Therefore, the periodic peaks in biomass shown in Figure 5b should be largely due to peaks at these or very similar sizes, which was indeed the case.

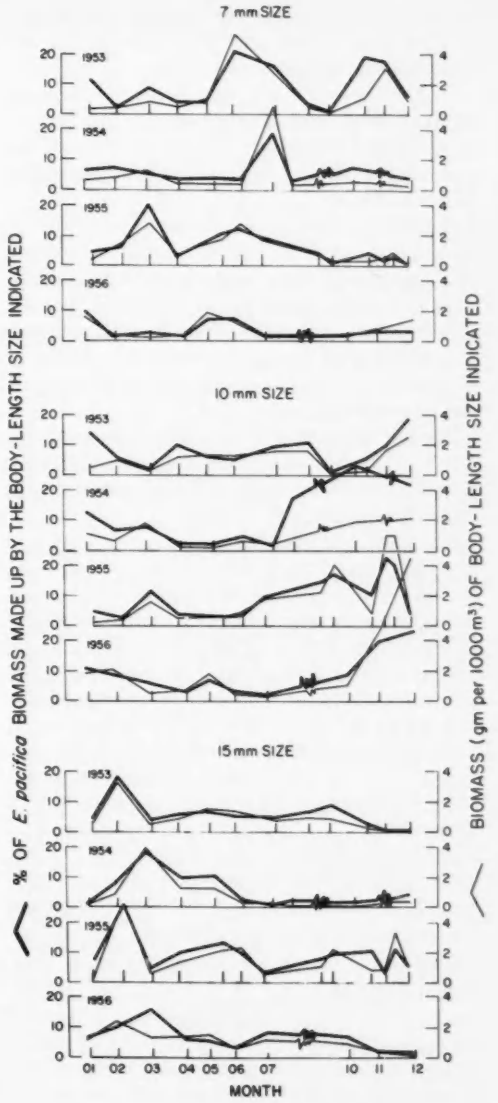
7 mm SIZE
10 mm SIZE
15 mm SIZE
1953
1954
1955
1956
% OF E. pacifica BIOMASS MADE UP BY THE BODY-LENGTH SIZE INDICATED
BIOMASS (gm per 1000 m³) OF BODY-LENGTH SIZE INDICATED
01 02 03 04 05 06 07 10 11 12
MONTH

FIGURE 17.—Annual length-biomass modes of *Euphausia pacifica* analyzed by months. The 7-mm size peaks heavily in June-July (May-June in 1956), with other peaks in March and November-January; the 10-mm size peaks September-January; and 15-mm size peaks February or March.

There are variations from this relationship: 1) moderate increase in biomass of 10-mm size during August-December 1954 caused a disproportionately large percent-increase in it—an effect of the single large 1954 cohort (5406-07) developing

unaccompanied by other substantial cohorts (Figure 16b); 2) the converse, when November-December 1955 biomass of 10-mm size (together with 11-12 mm, Figure 16c) increased extremely but the percent increase did not keep pace because of strong survival from extended July-September recruitment, seen as piling up in December across 8-12 mm range.

Rate of growth (body length) was seen, above, to be generally steady (Figure 12). Slowed growth was commonest when adolescence or late adulthood took place during fall-winter. Exceptionally high biomass of 10-12 mm sizes in 1955 and 1956 was attributed to greatly slowed growth of adolescents of large cohorts during November-December of both years.

Regular, less extreme peaking of biomass at the four body lengths just descibed as prominent may be interpreted in terms of differing survival rates among life phases:

If body-length growth is steady during a given life phase, such as the larval period, biomass growth would proceed as the cube of body length, while population size would be expected to decline exponentially. This inequality leads to a biomass peak at a particular body length which depends on survival rate (Figure 18a). A survival rate of about 24%/mo for the larval phase is found to yield such a peak at 4 mm length in the biomass on body-length distribution, a size at which biomass regularly peaks during *E. pacifica* development.

Other survival rates were extrapolated from a cluster of age-density curves so as to yield biomass peaks which coincide with real average peaks shown in Figure 16: 43%/mo was found to peak at 7 mm, 54%/mo at 10-11 mm, and 66%/mo at 15 mm. A derived age-biomass distribution, linear scale (Figure 18b), is composed of segments based on the above sequence of survival rates. Segments end at 5.8 mm (end of larval phase), 9.3 mm (end of juvenile phase), and 13.2 mm (start of intensive reproduction, after Figure 21b).

The derived distribution is similar in shape to the observed average annual biomass distributions for 1953 and 1954 (Figure 16a, b). (Growth rates of 1953 cohorts were relatively steady, Figure 12. Those of 1954 appeared less steady but were still without the massive November-December pile-ups of adolescents noted in 1955 and 1956.) However, except for the larval period for which the derived and observed mean survival rates (from Figure 14) were both about 23%/mo; other derived rates had to be different from the

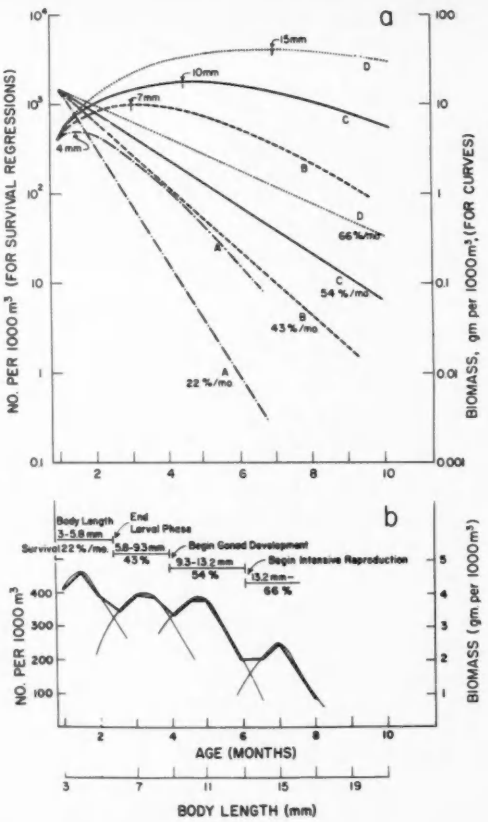

FIGURE 18.—Hypothetical age-frequency and age-biomass distributions of *Euphausia pacifica* assuming uniform body-length growth. a, Constant survivorship at each of four rates, selected to yield biomass peaking at 4, 7, 10, and 15 mm, respectively. b, An approximation of annual length-biomass distributions shown in Figure 17, obtained by changing survivorship at life-phase change.

mean observed rates so as to yield the observed peaks at 7, 10-11, and 15 mm length. These were lower by 24% and 10% for the juvenile and young adult phases respectively, and higher by 6% for the 14-18 mm sizes. This means that after the larval phase observed, mean survivorship decreased phase-to-phase by about 4%/mo, whereas in the derived distribution it increased by 11-12%/mo at phase change. This is attributed to deviations from evenness in real growth rates. However, there is a tendency toward progressively positive inflexion with age in certain of the survivorship curves of individual cohorts (Figure 15b-g).

Sex Ratio

Fifty percent of the estimates of prespawned eggs were two to four times greater than the estimates of larvae in the plankton a month later. The other 50% of egg/larva ratios were even lower than two (Figures 4d, 6). Further evidence that spawning was underestimated is seen in an examination of ratio of the sexes and state of their reproductive products.

The ripe male *E. pacifica* stores two spermatophores in a pair of ducts. The fertilized female possesses a single attached spermatophore (Brinton in press). This discrepancy might be attributed to a sex ratio in which females predominate, or to a need for more than one fertilization when spawning is protracted or intermittent across days, intermolt periods or longer. If such multiple fertilizations take place, males transfer one spermatophore to each of two females, probably quickly because single ripe spermatophores were not observed in males. The paired spermatophores in males were observed always to be of equal size, color, and readiness for extrusion. (Ready spermatophores may be easily expelled with gentle external pressure in the laboratory.) A continuing preponderance of ripe males, as shown in Figure 19, would tend to insure fertilization of females whenever they ripen. Mauchline and Fisher (1969) have explained, with reference to *Meganyctiphanes norvegica*, that fully formed spermatophores may be stored in the ejaculatory ducts for some time.

Here, ripe and unripe females outnumber males by about 1.5 times at 15 mm, and 3 times at 20 mm (See Figure 21a). Ponomareva's (1963) data on *E. pacifica* from the Sea of Japan showed females to be 56% of the adult population, and from the Okhotsk Sea 63% in April, 62% in June-July, and 44% in October. Four factors may contribute to the apparently greater number of females:

1) In the present data, apparent dominance by females (all body lengths lumped, Figure 20) is partly due to periods in which the population included late-maturing individuals of 10.5-11.5 mm length, some males of which were as yet without petasmas and were therefore categorized as females. (Secondary sexual characters of *E. pacifica* are usually evident at this size.) For example, this apparently happened during counting of material from cruises 5401 and 5402 (Figure 13), and cruises 5610-12 (Figure 20) when

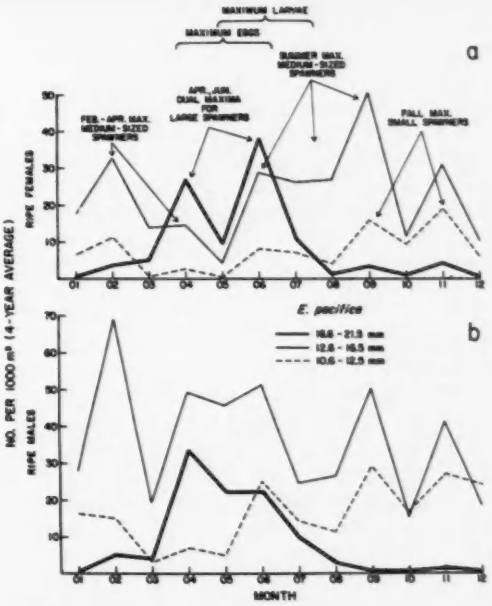

FIGURE 19.—a, Densities of ripe female *Euphausia pacifica* by months, three body-length groups, 1953-56 data combined from Figure 6d. b, Densities of males with ready spermatophores, same body-length groups.

"females" dominated the dense population of 8-12 mm individuals.

2) Increasing mortality in males relative to that in females may take place after 12 mm body length. Since the ratio of males to females decreases with body length, multiple fertilizations by males would be increasingly important with increasing size. (Mates are probably of similar size, in view of large spermatophores being attached to large females and small spermatophores to small females.)

3) Large males and unripe females may be more underestimated than egg-bearing females if the latter are less able to avoid net capture. For anchovy larvae, Isaacs (1965) hypothesized that avoidance of the 1-m net becomes significant after 15 mm body length. Similar differential avoidance might contribute to the female/male bias here. For 3 of the 4 yr, the average percentage of females that are ripe crested at 15-16 mm (Figure 21b). It remained high, 40-60%, through the larger size groups. The 1954 data differed in that the proportion of ripe/unripe females remained low through 16 mm body length. This is also seen in Figure 4d in which the 12.6-16.5 mm group showed

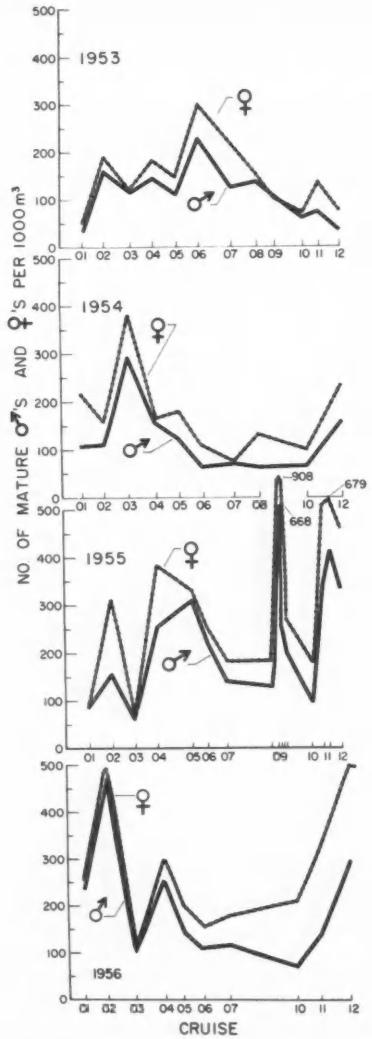

FIGURE 20.—Mean densities of presumed mature (>10.5 mm) male and female *Euphausia pacifica*, by month.

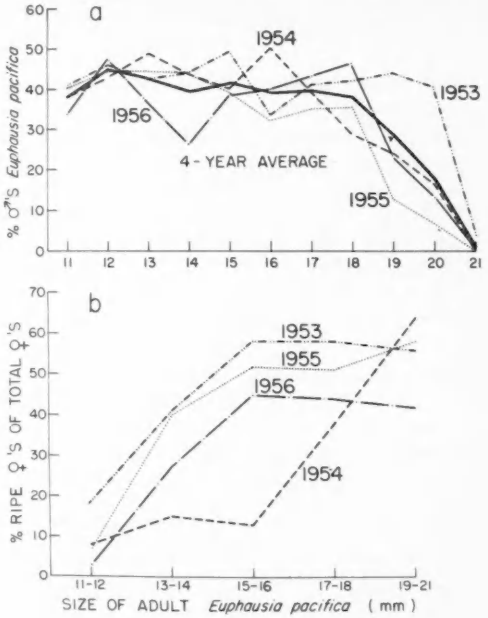

FIGURE 21.—a, Sex ratios for *Euphausia pacifica* by 1 mm body length, all data for each year averaged and 4-yr average. b, Annual gravidity ratios, by body length.

low reproductive activity. Furthermore, in 1954 the sex ratios for 13, 14, and 16 mm body length were 1:1, as compared with other years (Figure 21a). However, no relationship was seen (Figure 13) between numbers of gravid females of a given size and the difference between numbers of males and total females of the same size. Therefore, the observed increase with body length (at least to 15-16 mm) in the ratio of gravid to nongravid females appears natural, attributable either to higher frequency or longer duration of egg production with increasing body length.

4) An increase with body length in female/male ratio may be due to their differing growth rates. Both sexes tend to mature at the same size, ca. 11 mm. Thereafter, females grow slower, appearing increasingly numerous relative to males at successive body-length increments (Figures 14, 21a). Nemoto's (1957) data suggested that the adult male of *E. pacifica* tends to be smaller than the female of the same age, and Mauchline (1960) stated this to be the case in *Meganyctiphanes norvegica*. Slower growth rate in females indicates shorter life span for males, probably by 1 or 2 mo, since females grow to 21 mm length off southern California (rarely more) compared with 20 mm for males.

In summary, reasons were sought for a) underestimation of spawning, b) paired spermatophores in males, and c) apparent imbalance in sex ratio. These explanations were considered: eggs can ripen and females can spawn more often than the frequency of the surveys, applicable to a) and b); the bias in sex ratio favoring females is real and develops either with higher male mortality at

all sizes after maturity, applicable to b) and c), or because females grow slower and live longer, also applicable to b) and c); and the bias is an artifact of reduced net avoidance by ripe females and of observations during seasons when some males mature relatively late, resembly females for a time, applicable to c). Evidence supports each of the above. With regard to the increasing female/male ratio with body size, there are particularly strong indications of relatively slow growth in females, apparently leading to better survival than in males at given sizes and ages.

DISCUSSION

The predominance of *E. pacifica* among zooplankters off southern California appears related to the spring-early summer upwelling regime, which coincides with heaviest spawning. Recruitment consistently crested during May-July following annual surface temperature minima in April or May. Although this species may range southward along California and Mexico because of currents and the cool (10°-18°C) water, sole dependence on temperature effect in the southern California area for reproductivity is not likely because the area as a whole is coolest during December-April and the most substantial recruitment is later.

That the dependence is partly effected by food, as indicated by the seasonal pattern in availability of nutrients (plants), was shown in charts of the California Current region for 1969 for nutrients (Thomas and Seibert 1974) and for chlorophyll *a* (Owen 1974). The assumption is made that timing of the seasons in 1969 agrees enough with 1953-56 so that the April-June buildup in upwelling applies to both periods. Off southern California nutrient concentrations intensified in April and peaked in May in a patchy distribution corresponding to the areas of low surface temperature. For example, PO_4-P (integrated through 0-50 m depth) was in the range of 10-40 mg-at./m^2 during January-February and August-December but increased to 40-60 mg-at./m^2 during April-June. Silicate-Si peaked at 400-1,000 mg-at./m^2 during April-June; during the other months concentrations >400 mg-at./m^2 were rare.

Correspondingly, during the main upwelling period, April-September, chlorophyll *a* in the surface waters inhabited by newly hatched euphausiid larvae showed the patchy pattern of extreme concentrations shown also by the nutrients. Values peaked at 3.0 mg/m^3 during April-September compared with 2.0 mg/m^3 for January-March and 0.5 mg/m^3 for October-December. The possible importance of shallow (12-19.5 m), intense (to 50 μg/liter) chlorophyll maxima—particularly those containing the dinoflagellate *Gymnodinium splendens*—to first feeding of anchovy larvae was put forward by Lasker (1975). These maxima were found during March-April 1974 within 15 km of the southern California coast. Such layering of food particles could have broad significance to feeding and survival of zooplankton larvae.

Most larvae of *E. pacifica* are found in nearshore areas described above as recruitment refuges where upwelling prevails and currents are sluggish. Similarly, off Oregon (Smiles and Pearcy 1971), more larvae were in nearshore upwellings than in offshore water characterized by a summer productivity minimum typical of the region. Also working off Oregon, Peterson and Miller (1975) found no relationship between year-to-year (1969-71) intensity of summer upwelling and abundances of euphausiid eggs and larvae (not identified to species).

Evidence that larvae occupying southern California waters are produced locally is seen in the time of the upwelling season along the coast. Upwelling peaks off southern Baja California in February-March. Progressing northward, its maximum off Oregon is during August-September. Hence maximum spawning and recruitment, if upwelling induced, should develop along the same northerly track, counter to the direction of main flow in the California Current during this period of relatively consistent northeast winds. This is the case: recruitment off mid-Baja California, lat. 27°-29°N, is mainly February-April (Brinton 1967b, 1973), in Monterey Bay it is both spring and summer (Barham 1957), off southern California it is mainly May-July, and off Oregon, August-December.

Although ripening of ovaries, spawning, and recruitment reach maxima as consequence of upwelling-associated events, the southern California population includes ripe females and newly hatched larvae year-round (Figures 4c, d; 19). Off Oregon, *E. pacifica* also includes some larvae at all times (Smiles and Pearcy 1971); while in the Sea of Japan (lat. 40°-50°N) and south of Kamchatka, Alaska (lat. 50°-55°N), in areas enriched by winter mixing of the water column, *E. pacifica* possesses ripe gonads in May-June, the

presumed breeding period (Ponomareva 1963), though eggs were abundant in August nearby in the Sea of Okhotsk. To the north and south of the eastern Aleutian Islands, Nemoto (1957) found females of *E. pacifica* with attached spermatophores during July.

Dominance of the southern California population by the particular cohorts followed in the analyses of growth tends to obscure the regular contribution of small classes, including those of fall-winter in which densities of larvae are usually 1,000-2,000/1,000 m^3.

Such continuous recruitment of variable intensity is seen as an adaptation to midlatitude irregularity in oceanographic conditions, both seasonal and year-to-year, as compared with cycles at high latitudes. Continuous recruitment permits the stock to always include a wide spectrum of sizes and maturity stages, providing a potential for one or another to adapt to periods of poor climate or food availability, of differing duration or amplitude. For example, in 1954, a year of weak upwelling, recruitment was all but limited to June-July; nevertheless, spawning resumed at high intensity during four different periods in 1955.

Periodicity was observed in maxima of spawning and recruitment, and recruitment is appropriately out of phase with the inferred spawning (Figure 4c), implying substantial synchrony among breeders. Spawning apparently pulses at a 2-mo frequency during the period of maximum gamete generation, which also must be the period of maximum food use by breeders and larvae. This is to be compared with the annual (or at most, semiannual) frequency of breeding noted in the subarctic North Pacific. Thus it appears possible that, under optimal feeding conditions off southern California, a female might spawn every 2 mo: first at about 11.5 mm length (20-50 eggs), second at 16 mm (50-200 eggs), and third at 20 mm (100-400 eggs), during which time an individual might be expected to produce a maximum of 650 eggs. This is compatible with an observation of 1,400 oocytes (all stages of development) in ovaries of an *E. pacifica* in the springtime in the northeastern Pacific (Ponomareva 1963) where spawning is concentrated into one season, and with Lasker's observation, reported in Mauchline and Fisher (1969), that an *E. pacifica* from southern California shed 230 eggs after capture.

The long duration of maturity—probably half of this species' life expectancy—further contributes to population stability and continuity. In conjunction with substantial horizontal transport, the capacity to breed several times enhances genetic integration across the distributional range.

The first observations on growth in *E. pacifica* were from specimens maintained in the laboratory by Lasker (1966) at 10°C with excess food. In small juveniles, growth was steady at 2.5 or 2.9 mm during 2 mo, from about 5 to 8 mm length. In the southern California field populations, growth of juveniles of this size was consistently in the range of 3-3.5 mm/mo. However, the 5309 cohort, having reached 5 mm by the start of the fall period of reduced growth, then grew only 3 mm in 1.5 mo.

Larger *E. pacifica* were observed by Lasker to grow somewhat slower. A 6.5-mm specimen grew 1.5 mm in 70 days, but added only 1.5 mm in 230 more days before dying, not having reached fully adult size. A 7.9-mm specimen grew 1.5 mm in 75 days, an 8.0-mm specimen grew 1.5 mm in 130 days, and an 8.4-mm specimen grew 1.0 mm in 160 days. These rates are smaller than those for the local field populations. They are closer to those supposed for *E. pacifica* in the northeastern Pacific where environmental enrichment is not by intermittent upwelling but by winter mixing followed by spring stability in the water column, hence not a continuing process.

In the analysis of growth, cohorts are considered as normal L-F distributions representing broods continuously hatched during a few days to a month or more. Observation on duration of reproduction is limited by the character of the sampling, here in approximately 1-wk period with a 2-3 wk interval between surveys. Only in a few of the months can a pulse in recruitment by recognized as distinct to that month. In most months, the larvae derive from the beginning, continuation, or end of a period of cohort formation which extends beyond one survey period and into another. Recruitment found less than in past or succeeding months is neither recognizable initially as a cohort nor traceable thereafter.

The area's population, therefore, is constantly polymodal in character, being compounded of individuals belonging to different age-groups and sexes. The possible difference in size between the sexes after about 15 mm length was not taken into consideration in the growth study.

The simplest method of analyzing growth and survival is that of following obvious modes, survey to survey. This is probably the most significant means biologically. Nevertheless, certain im-

precise trends in development of presumed cohorts provide growth rates which corroborate the more obvious trends. Some pathways of development indicated in Figures 9 and 10 may appear imaginary unless the shapes and amplitudes of the related L-F distributions, adjacent in time, are closely compared. When such indistinct modes are followed, precision and accuracy in recognizing rates of development are reduced. Graphical procedures for mathematically defining cohorts composing irregular L-F polygons (e.g., Harding 1949) required some subjectivity in recognizing modes and were employed only in an exploratory way.

There can be important inaccuracies in field estimates of growth rate when reliance is upon time-sequences in L-F modes. Even with steady, uniform recruitment, peaks or troughs would appear in the L-F distribution owing to differing growth rates and survivorship among life phases or between sexes. With unsteady recruitment, such peaks may sometimes lie in phase with the cohort being traced, but the cohort nevertheless becomes compounded by younger individuals when its growth is differentially slowed or by older individuals when accelerated.

It is possible that the individuals composing a mode could be totally replaced in the course of its time progression, although the modal assemblage persists as a size group, presumably feeding and mating as a unit. I have noted above that spring-summer cohorts tend to "pile up" in fall-winter when growth of adolescents appears to be food limited.

In tracing growth, reliance is therefore upon the more substantial cohorts. Although these can be masked, their frequent appearance as modes at sizes not associated with life-phase changes gives credence to the method.

Growth rates of *E. pacifica* off southern California appear similar to those off Oregon (Smiles and Pearcy 1971). Figure 22 shows generalized growth curves for this species from four areas in the North Pacific. The Oregon population showed steady growth after September recruitment. The juvenile and adolescent phases were during the winter and 13 mm was reached by February. About 22 mm was attained after 1 yr. This parallels development of a winter cohort (5512) off southern California which grew to 12 mm in 3 mo and was traced to about 21 mm after 8 mo.

Spring (5406) and summer (5309) cohorts off southern California grew at rates similar to the

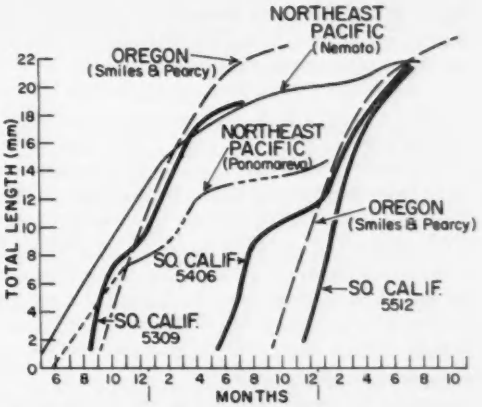

FIGURE 22.—Representative growth curves from southern California area compared with curves previously derived for *Euphausia pacifica* and illustrated by Smiles and Pearcy (1971).

winter cohort, except for slowing during October-December—5406 during adolescence and 5309 during the juvenile phase.

Here, life expectancy appears to be about 8 mo for winter and early-spring cohorts, to sizes of 18-20 mm by August-October. December-January populations never included individuals larger than 19 mm. Life expectancy is up to 12 mo for late-spring and summer cohorts, which grew to 21-22 mm by the following April-July. This agrees with estimates of 12 mo for September cohorts off Oregon.

Growth in other euphausiid species, mostly summarized in Smiles and Pearcy (1971), is similar. Several reach about 22 mm after 1 yr: *E. superba* (Ruud 1932; Bargmann 1945; Marr 1962), *E. triacantha* (Baker 1959), *Thysanoessa raschii* (Mauchline 1966), *Meganyctiphanes norvegica* (Ruud 1936; Einarsson 1945; Mauchline 1960; Matthews 1973), and *Thysanopoda acutifrons* (Einarsson 1945). Most of these species have a life expectancy of 2 yr, reproducing in each and growing slowly or not at all in winter.

During winter in the westernmost North Pacific (Sea of Okhotsk), Ponomareva (1963) found *E. pacifica* to be 8 mm (considered to have hatched the previous summer) and 14-15 mm (considered 2 yr old). In the spring it was 12-13 mm (1 yr old) and 19 mm (2 yr old). Both groups bred in June. Off nearby Kamchatka in the summer, Nemoto (1957) found a size range of 12-22 mm, much like that found by Ponomareva, but with most at 14-20 mm. There were no larvae, but females with spermatophores were present in September, as off Oregon.

South of the Aleutian Islands in September, he found a 6-12 mm group interpreted as having hatched in the spring or early summer. Maximum numbers of adult females were 16-19 mm in May, 17-21 mm in June, and 18-22 mm in September.

Thus growth of *E. pacifica* is inferred to be slower and of longer duration in the Subarctic seas than off Oregon and California (Figure 22). Nemoto's (1957) estimate from south of the Aleutians was intermediate between Ponomareva's (1963) from the western Pacific and those from the American coast. Ponomareva's finding that sexual maturity is attained by 15-17 mm, with some mature at only 11-12 mm, agreed with the observations off southern California.

During *E. pacifica*'s main reproductive season there is similarity in surface water temperatures (Sverdrup et al. 1942; Anonymous 1963) among the five North Pacific areas from which information on life history comes; there is less agreement in winter temperatures:

Sea of Okhotsk	10-13°C (Aug.),	0°C (Feb.)
Off Kamchatka	9-11°C (Aug.),	0°- 1°C (Feb.)
South of Aleutians	10-12°C (Aug.),	2°- 4°C (Feb.)
Off Oregon	10-14°C (Sept.),	9°-11°C (Feb.)
Off southern California	10-18°C (June),	12°-15°C (Feb.)

Winter temperatures in the three subarctic areas are near 0°C whereas off Oregon and California they differ little from spring-summer temperatures influenced by upwelling. An overall temperature regime for *E. pacifica* is thereby described in which low temperature does not limit occupancy but in which 9°-16°C is suitable for reproduction, food permitting. In the subarctic region reproduction takes place at 9-13°C, the highest annual temperatures there. To the south of the California Current off mainland Mexico, food seems to be abundant, but other factors (temperatures >20°C, oxygen concentrations <0.1 ml/liter, different current systems) appear there to curtail the species' range.

The serial biomass representations included here clearly show rise and decline of cohorts, but are less exact than length frequency in determining growth and do not serve in estimating survivorship. It is evident that biomass of the species fluctuates month-to-month, with recruitment and growth not balancing mortality in any regular way. However in 34 of the 48 mo, the biomass was within the range of 8-22 g/1,000 m^3.

The intense densities of *E. pacifica* at 8-12 mm, also appearing as conspicuous biomass peaks, are the rule rather than the exception. Therefore, such regular concentrating at the adolescence interphase, particularly in fall-winter, may be other than an incidental consequence of reduced food. It appears as a means of increasing size uniformity in the population, hence improved breeding efficiency, by the time of the spring bloom—a condition fulfilled by stricter seasonality in the high-latitude populations of *E. pacifica*.

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LITERATURE CITED

AHLSTROM, E. H.
1948. A record of pilchard eggs and larvae collected during surveys made in 1939 to 1941. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 54, 75 p.

ANONYMOUS
1963. CalCOFI atlas of 10-meter temperatures and salinities 1949 through 1959. Calif. Coop. Oceanic Fish. Invest., Atlas 1, 297 p.

BAKER, A. DE C.
1959. The distribution and life history of *Euphausia tricantha* Holt and Tattersall. Discovery Rep. 29:309-340.

BAKUN, A.
1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.

BARGMANN, H. E.
1945. The development and life-history of adolescent and adult krill, *Euphausia superba*. Discovery Rep. 23:103-176.

BARHAM, E. G.
1957. The ecology of sonic scattering layers in the Monterey Bay area, California. Ph.D. Thesis, Stanford Univ., 192 p.

BODEN, B. P.
1950. The post-naupliar stages of the crustacean *Euphausia pacifica*. Trans. Am. Microsc. Soc. 69:373-386.

BRINTON, E.
1960. Changes in the distribution of euphausiid crustaceans

in the region of the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 7:137-146.

1962a. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr., Univ. Calif. 8: 51-269.

1962b. Two new species of Euphausiacea, *Euphausia nana* and *Stylocheiron robustum* from the Pacific. Crustaceana 4:167-179.

1967a. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12:451-483.

1967b. Distributional atlas of Euphausiacea (Crustacea) in the California Current Region, Part I. Calif. Coop. Oceanic Fish. Invest. Atlas 5, 275 p.

1973. Distributional atlas of Euphausiacea (Crustacea) in the California Current region, Part II. Calif. Coop. Oceanic Fish. Invest. Atlas 18, 336 p.

In press. Observations of spermatophores attached to pleopods of male euphausiids. Crustaceana.

BRINTON, E., AND J. G. WYLLIE.

In press. Distributional atlas of Euphausiacea, Part III. Developmental stages of euphausiids in the region of the Southern California eddy, 1953-1956. Calif. Coop. Oceanic Fish. Invest., Atlas 24.

CHILDRESS, J. J.

1971. Respiratory rate and depth of occurrence of midwater animals. Limnol. Oceanogr. 16:104-106.

EINARSSON, H.

1945. Euphausiacea. 1. North Atlantic species. Dana Rep. Carlsberg Found. 27, 185 p.

FOWLER, S. W., L. F. SMALL, and S. KEČKEŠ.

1971. Effects of temperature and size on molting of euphausiid crustaceans. Mar. Biol. (Berl.) 11:45-51.

GILFILLAN, E.

1972. Reactions of *Euphausia pacifica* Hansen (Crustacea) from oceanic, mixed oceanic-coastal and coastal waters of British Columbia to experimental changes in temperature and salinity. J. Exp. Mar. Biol. Ecol. 10:29-40.

GOPALAKRISHNAN, K.

1973. Developmental and growth studies of the euphausiid *Nematoscelis difficilis* (Crustacea) based on rearing. Bull. Scripps Inst. Oceanogr., Univ. Calif. 20:1-87.

HARDING, J. P.

1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. Biol. Assoc. U.K. 28:141-153.

HARDY, A. C.

1956. The open sea. Its natural history: the world of plankton. Houghton Mifflin Co., Boston, 335 p.

ISAACS, J. D.

1965. Larval sardine and anchovy interrelationships. Calif. Coop. Oceanic Fish. Invest. Rep. 10:102-140.

LASKER, R.

1964. Molting frequency of a deep-sea crustacean, *Euphausia pacifica*. Nature (Lond.) 203:96.

1966. Feeding, growth, respiration, and carbon utilization of euphausiid crustacean. J. Fish. Res. Board Can. 23:1291-1317.

1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.

MARR, J.

1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). Discovery Rep. 32:33-464.

MATTHEWS, J. B. L.

1973. Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Population dynamics of *Meganyctiphanes norvegica* (Crustacea, Euphausiacea) in 1968 and 1969. Sarsia 54:75-90.

MAUCHLINE, J.

1960. The biology of the euphausiid crustacean, *Meganyctiphanes norvegica* (M. Sars). Proc. R. Soc. Edinb., Sect. B., Biol. 67:141-179.

1966. The biology of *Thysanoessa raschii* (M. Sars), with a comparison of its diet with that of *Meganyctiphanes norvegica* (M. Sars). *In* H. Barnes (editor), Some contemporary studies in marine science, p. 493-510. George Allen and Unwin Ltd., Lond.

1968. The development of the eggs in the ovaries of euphausiids and estimation of fecundity. Crustaceana 14:155-163.

MAUCHLINE, J., AND L. R. FISHER.

1969. The biology of euphausiids. Adv. Mar. Biol. 7, 454 p.

MILLER, J. K.

1966. Biomass determinations of selected zooplankters found in the California Cooperative Oceanic Fisheries Investigations. Scripps Inst. Oceanogr. SIO Ref. 66-15, 18 p.

NEMOTO, T.

1957. Foods of baleen whales in the northern Pacific. Sci. Rep. Whales Res. Inst. 12:33-90.

OWEN, R. W., JR.

1974. Distribution of primary production, plant pigments and Secchi depth in the California Current region, 1969. Calif. Coop. Oceanic Fish. Invest. Atlas 20:xi-xiv, charts 98-117.

PARANJAPE, M. A.

1967. Molting and respiration of euphausiids. J. Fish. Res. Board Can. 24:1229-1240.

PEARCY, W. G., AND L. F. SMALL.

1968. Effects of pressure on the respiration of vertically migrating crustaceans. J. Fish. Res. Board Can. 25:1311-1316.

PETERSON, W. T., AND C. B. MILLER.

1975. Year-to-year variations in the planktonology of the Oregon upwelling zone. Fish. Bull., U. S. 73:642-653.

PONOMAREVA, L. A.

1963. Euphausiids of the North Pacific, their distribution and ecology. Akad. Nauk SSSR Inst. Okeanol. (Translated by Israel Program for Scientific Translations, Jerusalem 1966, IPST Catalog No. 1368, 154 p.)

REID, J. L., JR., G. I. RODEN, AND J. G. WYLLIE.

1958. Studies of the California Current system. Calif. Coop. Oceanic Fish. Invest., Prog. Rep., 1 July 1956 to 1 Jan. 1958, p. 27-57.

RUUD, J. T.

1932. On the biology of southern Euphausiidae. Hvalradets Skr. 2, 105 p.

1936. Euphausiacea. Rep. Dan. Oceanogr. Exped. 1908-1910 Mediter. Adjacent Seas 2D6 (Biol.), 86 p.

SMALL, L. F.

1967. Energy flow in *Euphausia pacifica*. Nature (Lond.) 215:515-516.

SMALL, L. F., AND J. F. HEBARD.

1967. Respiration of a vertically migrating marine crustacean *Euphausia pacifica* Hansen. Limnol. Oceanogr. 12:272-280.

SMALL, L. F., J. F. HEBARD, AND C. D. MCINTIRE.
1966. Respiration in euphausiids. Nature (Lond.) 211:1210-1211.

SMILES, M. C., JR., AND W. G. PEARCY.
1971. Size structure and growth rate of *Euphausia pacifica* off the Oregon coast. Fish. Bull., U.S. 69:79-86.

SMITH, P. E.
1971. Distributional atlas of zooplankton volume in the California Current region, 1951 through 1966. Calif. Coop. Oceanic Fish. Invest., Atlas 13: v-xvi, 144 p.

SOUTH PACIFIC FISHERY INVESTIGATIONS.
1954. Zooplankton volumes off the Pacific Coast, 1953. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 132, 38 p.
1955. Zooplankton volumes off the Pacific coast, 1954. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 161, 35 p.
1956. Zooplankton volumes off the Pacific coast, 1955. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 177, 32 p.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING.
1942. The oceans, their physics, chemistry and general biology. Prentice Hall, N.Y., 1087 p.

THOMAS, W. H., AND D. L. R. SEIBERT.
1974. Distribution of nitrate, nitrite, phosphate and silicate in the California Current region, 1969. Calif. Coop. Oceanic Fish. Invest., Atlas 20:vii-x, charts 2-97.

THRAILKILL, J. R.
1957. Zooplankton volumes off the Pacific coast, 1956. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 232, 50 p.

UDA, M., AND M. ISHINO.
1958. Enrichment pattern resulting from eddy system in relation to fishing grounds. J. Tokyo Univ. Fish. 44:105-119.

WYLLIE, J. G.
1966. Geostrophic flow of the California Current at the surface and at 200 meters. Calif. Coop. Oceanic Fish. Invest. Atlas 4, 288 p.

PRODUCTION OF JUVENILE CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, IN A HEATED MODEL STREAM[1]

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ABSTRACT

Temperature was elevated approximately 4°C in a model stream, compared with an unheated but otherwise similar control stream. The streams were located outdoors and received identical amounts of exchange water from a nearby creek. Diel and seasonal temperature fluctuations were similar to those of area streams. Juvenile spring chinook salmon, *Oncorhynchus tshawytscha*, were introduced into each stream either as eyed eggs or fry and allowed to remain for approximately 1 yr. Two consecutive year classes of juvenile salmon were studied. Their production was measured triweekly and related to changes in temperature, food availability, and other environmental factors. Ancillary experiments utilizing water from the model streams permitted measurement of differences in growth rate of salmon fed various rations.

Salmon production in the control stream exceeded that in the heated stream. In 1972, total production in the control stream was twofold greater and, in 1973, it was approximately 30% greater than in the heated stream. Elevated temperature resulted in reduced growth rates of the fish especially as food became less abundant and at times also resulted in lower biomasses of food organisms, either because the temperature increase directly affected survival and growth of benthic invertebrates or because increased sedimentation associated with heavier growth of filamentous algae made riffle substrate less suitable for certain species. Beneficial effects of increased temperature appeared to include protection from infestation by a trematode parasite (*Nanophyetus salmincola*) and, possibly, increased tendencies of some invertebrates to enter the drift.

Studies of the effects of elevated temperature on stream dwelling organisms have been largely confined to short-term laboratory experiments or to field surveys associated with man-caused thermal increases. We have employed two large model streams, one heated and one unheated, to examine the effects of constantly elevated temperature on production of juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), under conditions similar to natural streams, but where temperature could be controlled. Identifying the factors governing productivity of the streams that were influenced by increased temperature and measuring the impact of the addition of a known amount of heat on chinook salmon production were the two main objectives of the research.

Temperature change can affect salmonid fishes in two general ways. First are the direct effects, e.g., accelerated developmental rates, altered food conversion efficiencies, and, under certain conditions, lethality. These kinds of effects have received considerable attention in laboratory experiments. Less well understood are the indirect effects, one of the most important being resultant changes in the abundance of food organisms. In a previous study involving the same streams, Iverson (1972) found that the production of juvenile coho salmon, *O. kisutch*, was significantly reduced in the heated stream compared with the unheated control, and he attributed this reduction mainly to lower biomasses of immature stages of insects in the heated stream. Evaluating the importance of indirect consequences of temperature elevation on juvenile chinook thus became one of our major concerns, for water quality guidelines relating to the temperature requirements of salmon and trout are based primarily upon knowledge of direct effects and to a much lesser extent upon possible indirect or secondary effects.

MATERIALS AND METHODS

Physical Characteristics of the Streams

The model streams were located at the Oak Creek Laboratory of Biology near Corvallis in

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western Oregon. They consisted of two large wooden channels interconnected at the ends by pipes (Figure 1). Within each stream were four riffle-pool sections of equal size; the total surface area available to fish and other organisms was 22 m^2. Minor differences in substrate composition, water velocity and depth, and shading from terrestrial vegetation existed among the riffle-pool sections. These variations were sufficient to prevent the sections from being treated as replicates; therefore, samples from each of the four sections were composited.

The slope of each stream was approximately 1.9% so that water pumped into the upstream ends flowed downstream at velocities typical of natural streams (approximately 60 cm/s in the riffles to near 0 cm/s at the bottom of the pools). A 2-horsepower centrifugal pump forced water from the downstream end of one channel to the upstream end of the other. A gate valve controlled the flow rate, which was maintained at approximately 1.35 m^3/min.

Complete freedom of movement for the fish was allowed between the two channels. Individuals could pass downstream or upstream through the pipe from one side to the other; they were, however, prevented from entering the pump by a screen at the downstream end of the lowermost pool. Movement of the fish from the streams took place through a 6-cm diameter outlet pipe that originated at the screen and terminated in a partitioned trap. Fish that entered the trap were returned to the uppermost riffle both to avoid fortuitous losses and to provide the fish with an adequate opportunity to establish residence.

Substrate consisted of a layer of rocks approximately 7 cm deep. Following Cummins' (1962) terminology, cobbles and pebbles composed more than 95% of the substrate, both in the riffles and pools, while larger sand was almost absent. No large boulders were present, although a few cobbles projected above the water. A difference in the amount of very fine sediments existed between the two streams; this difference will be discussed in connection with their invertebrate faunas.

Temperature Regulation

Water temperature in the unheated control followed natural diel and seasonal cycles (Figure 2). Two 6-kw stainless steel heaters regulated by a variable input timer facilitated temperature elevation in the heated stream. Continuous recordings of the temperature were made by Partlow RFT thermographs.[4] Differences between monthly means ranged from 3.3°C (August 1972) to 4.9°C (December 1972): the average temperature difference between the streams was 3.9°C.

Both streams received 10-20 liters/min of unfiltered water from a small spring-fed creek that contained aquatic invertebrates and algae, but no fishes. During periods of low stream flow, the water supply was supplemented by a mixture of well water and unfiltered water pumped from a large nearby creek. The model streams have been operating continuously at approximately the same temperature differential since completion of construction in 1969 (Iverson 1972). However, in December 1972 unusually cold weather caused

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

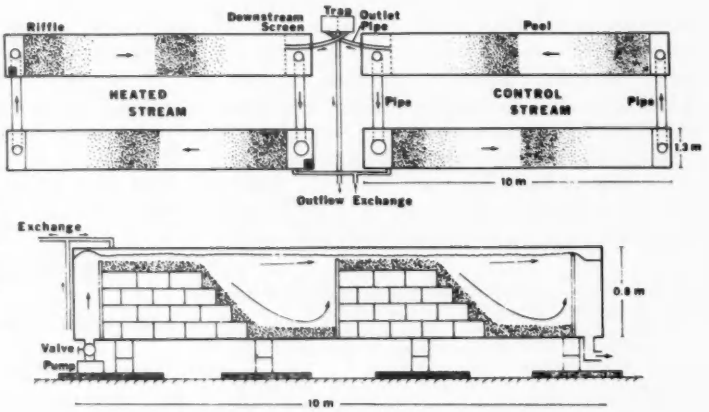

FIGURE 1.—Top. Plan view of model streams. Arrows indicate direction of water flow and black squares in the heated stream denote location of heating units. Bottom. Cross section of one of the channels in a model stream.

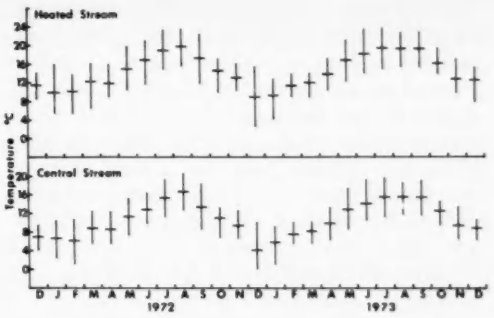

FIGURE 2.–Temperature conditions in the model streams. Horizontal and vertical lines represent monthly means and ranges, respectively.

glass observation windows in the control stream to break; as a result, the entire riffle substrate was exposed for several days while new windows were being installed and some losses of periphyton and invertebrates occurred. One window was also replaced in the heated stream at this time, necessitating exposure of one riffle.

Associated Flora

Vegetation surrounding the streams included red alder, *Alnus rubra*, and apple, *Malus* sp. These trees contributed leaves, catkins, and flowers as well as a variety of terrestrial invertebrates.

Periphytic algae composed the bulk of living plant material within the streams. The same plant species were found in both heated and control streams, although differences in biomass and temporal succession occurred. The dominant species from late spring to fall was *Cladophora glomerata*, a filamentous green alga that attached to large particles in the riffles and often trailed into pool areas. Various diatoms also made up a significant proportion of the flora. Two species exhibited especially heavy seasonal blooms. In early spring, filaments of a colonial diatom, *Melosira varians*, covered both riffles and pools; this species was noticeably more common in the control than in the heated stream. In summer and fall *Synedra ulna* became the dominant diatom, occurring both in the water mass and among living and dead algae on the bottom. Blue-green algae were generally found in late spring and summer. *Calothrix* and *Nostoc* were more abundant and appeared earlier in the heated stream than in the control. An unidentified dense moss colonized some of the large cobbles in the riffles. Diatoms and desmids, in addition to plant materials from terrestrial sources, were common in the drift. The desmid *Closterium lunula* was abundant in spring and early summer and was found to be an important food resource for filter-feeding invertebrates.

Benthos and Drift

Benthic plants and animals were sampled triweekly. Wire mesh baskets 20 × 20 × 6 cm painted with nontoxic paint and having wood bottoms were filled with substrate and placed against supporting blocks in the riffles. The mesh size (2 cm) was small enough to retain most of the particles and large enough to allow movement of invertebrates into and out of the baskets. Each riffle in the streams contained four baskets placed about 1 m apart from upstream to downstream end. One basket was selected from a different location in each riffle, the contents emptied into a bucket, and all large particles cleaned with a plastic scrub brush. The combined samples from four baskets (0.16 m^2 total) were then collected in a 200-μm mesh bag. One sample was taken from a pool in each channel, and collected material was combined and preserved in 10% Formalin.

Drifting organisms were collected triweekly by means of 333-μm mesh drift nets (Anderson 1967) that were suspended at the downstream end of the riffles. Two nets were fished in each stream (one per channel) for a 24-h period. Samples were removed and preserved at approximately sunrise and sunset so that diel differences in drift rates could be measured. Current velocity was measured at each sampling position and the amount of water passing through the nets during an interval was determined by multiplying this velocity by the cross sectional area of the water (330 cm^2) at the mouth of the net. During periods when considerable masses of leaves or algae were present in the drift, usually late summer and fall, some clogging took place and the volume of water entering the nets was overestimated.

All samples were allowed to remain in Formalin for 1 or 2 days, after which they were washed briefly with water. Drift samples were transferred directly to 70% ethanol prior to enumeration, while bottom samples were first sorted to remove invertebrates larger than 4 mm, and then subsampled (10% by volume) and preserved in ethanol. All organisms were measured to the nearest millimeter by means of a metric grid placed on the stage of the microscope. We assumed that no

length changes occurred during preservation. The number of individuals for each species in each size interval was recorded for every sample.

The remaining 90% of a bottom sample—that not sorted under magnification—was dried at 70°C for 4 days and then ashed at 600°C. Ten percent of its organic weight was arbitrarily assumed to have been lost during preservation. Subtracting the estimated biomass of small (<4 mm) invertebrates within this subsample from the total loss of ignition yielded the ash-free dry weight of filamentous algae, some diatoms, detritus, and organisms too small to be seen during the sorting process. Conversion to energy units (kcal) was accomplished by multiplying the plant-detritus biomass by 4.05, the mean of five samples combusted in an oxygen bomb calorimeter.

Computations of invertebrate biomasses were based on live specimens collected from a nearby stream, grouped according to size and species, and weighed after drying 4 days at 70°C. Their average dry weights were converted to calories by values obtained from Cummins and Wuycheck (1971) or determined directly by calorimetry. When no representatives of a certain size were available, a value for that interval was estimated by interpolation. Very similar forms were assumed to have identical values. For bottom samples, the biomass (kcal/m^2) of each size class of each taxon was taken as the product of the number of individuals in that class, the estimated caloric value for individuals of that size, and the appropriate area conversion factor. The product of the number of individuals and the caloric value was divided by the total amount of water passing through the nets to give biomass estimates per unit volume (cal/m^3) for the drift samples. Summing the values of all size intervals gave the total caloric content for each taxon.

Fish

Fertilized chinook salmon eggs were obtained from the Marion Forks Salmon Hatchery of the Oregon Department of Fish and Wildlife. Eggs for the 1972 experiment, taken 3 October 1971, were from a single pair mating. Eggs used in the 1973 experiment, taken 1 October 1972, were obtained by crossing three females with four males. This was done in order to increase genetic heterogeneity among fish in the 1973 experiment. Following fertilization, the eggs were transported immediately to holding facilities where they were incubated at 12°C.

In 1971, eggs were introduced into the streams when they reached the eyed stage. They were hatched in floating baskets and the fry were released shortly before yolk absorption was completed. Owing to accelerated development in warmer water, fish in the heated stream were released sooner than those in the control, although the initial number of individuals placed in the two streams was identical (425). A 10-wk recolonization period following repairs delayed introduction of salmon until mid-March 1973, when 200 fry were released simultaneously into each stream.

When the fish had reached approximately 0.4 g wet weight, they were all removed from the streams for measurement of individual length and weight every 3 wk until an experiment was terminated. From 5 to 20 fish were randomly drawn from the populations for stomach analyses. A blunted 22-gauge needle on a 5-ml syringe was inserted through the esophagus of an anesthetized fish into the anterior limb of the stomach. Several milliliters of water were gently injected into the stomach, forcing the contents out through the mouth into a collecting beaker. The combined whole food organisms and identified fragments of each taxon were weighed to the nearest 0.1 mg, and each taxon was assigned a percentage of the diet based on its fraction of the total wet weight of the sample.

Direct effects of the model stream temperature regimes on chinook salmon growth rates at different levels of food availability were studied in concurrent experiments. Fish of the same parentage and size as those in the model streams were placed in insulated streamside troughs, where they were fed live *Tubifex* at rations ranging from near maintenance to near repletion. The troughs received water directly from the model streams, and temperature differences between the troughs and streams were never greater than 0.3°C. Ten-day growth experiments were carried out once each season during 1973. Each experiment was preceded by a 10-day period of acclimation to temperature and ration size. Numbers of individuals tested at each ration level ranged from 10 to 20 depending upon fish size.

Average relative growth rates (Warren 1971) of the salmon were calculated as:

$$ARG = \frac{\bar{W}_2 - \bar{W}_1}{0.5\,(\bar{W}_1 + \bar{W}_2) \cdot t}$$

where ARG represented growth, $\bar{W}_1$ and $\bar{W}_2$

represented the mean weights of the fish at the beginning and end of the sampling interval, and t was the sampling interval in days. Growth was assumed to be linear over the relatively short 3-wk period. Relative growth rates, which were essentially the same as instantaneous growth rates, were considered more appropriate for comparison with relative food consumption rates.

Average biomass ($\bar{B}$) was calculated as:

$$\bar{B} = \frac{B_1 + B_2}{2}$$

where B_1 and B_2 represented the total weights of the fish at the beginning and end of the sampling interval.

Production during each sampling interval was calculated as the product of average relative growth rate (ARG) and average biomass ($\bar{B}$).

The conversion of wet weights to calories was accomplished by relating caloric content of tissue to condition factors of the fish, where condition factor was taken as 100 times a fish's weight (g) divided by the cube of its fork length (cm). Figure 9 of Warren et al. (1964:630), describing this relationship for cutthroat trout, *Salmo clarki*, was used for graphical estimates of calories per gram of wet weight for juvenile chinook salmon.

RESULTS

Temporal Changes in Production

Total production of chinook salmon in the heated stream was less than half that of the control in 1972 (Table 1). During the following year, production in the control stream was approximately 30% higher than in the heated stream. Mortality was greatest immediately after release into the streams, with populations attaining fairly stable levels by late summer. Population biomasses rose during winter and spring, were highest during late spring, and gradually declined through summer and fall. The mean annual biomass in the

TABLE 1.—Mean production statistics of experimental chinook salmon populations. H = heated stream, C = control stream.

Time interval	Individual size (kcal)		Population size (no.)		Mortality rate (%/day)		Biomass (kcal/m²)		Growth rate (cal-kcal/day)		Production (kcal/m²)	
	H	C	H	C	H	C	H	C	H	C	H	C
1972:												
20 Dec. -24 Jan.	0.31		302		1.61		4.12		1.85		0.27	
25 Jan. -14 Feb.	0.49		169		0.46		3.09		21.48		1.39	
15 Feb. - 7 Mar.	0.84	0.48	140	358	1.22	0.62	4.20	7.24	26.50	3.08	2.23	1.14
8 Mar. -27 Mar.	1.18	0.92	112	271	0.74	0.81	5.14	8.62	16.00	33.03	1.73	5.42
28 Mar. -15 Apr.	1.41	1.32	91	233	1.23	0.73	5.38	11.91	9.31	19.21	0.95	4.26
16 Apr. - 6 May	2.18	2.01	65	184	1.63	1.39	5.32	14.04	23.80	47.42	2.27	5.89
7 May -27 May	2.77	2.79	47	145	0.92	0.50	5.29	15.82	11.35	15.48	1.26	5.14
28 May -16 June	3.61	3.36	40	125	0.48	0.84	5.80	17.61	13.17	9.27	1.53	3.27
17 June - 7 July	4.36	3.75	34	105	0.88	0.75	6.25	16.97	8.96	5.22	1.18	1.86
8 July -28 July	4.53	4.32	31	92	0.01	0.35	6.26	16.97	1.82	6.73	0.24	2.40
29 July -22 Aug.	4.82	4.35	26	85	1.24	0.34	5.26	16.65	2.48	0.28	0.34	0.12
23 Aug. - 8 Sept.	5.68	4.74	19	67	0.84	2.03	4.65	13.84	9.64	5.05	0.76	1.19
9 Sept.- 3 Oct.	5.79	5.01	17	52	0.22	0.15	4.56	11.52	0.77	2.22	0.09	0.64
4 Oct. -19 Oct.	5.61	5.76	16	48	0.74	0.61	4.15	11.87	−1.44	9.29	−0.13	1.65
20 Oct. - 7 Nov.	6.15	5.73	14	46	0.35	0.01	3.88	12.01	4.83	−0.27	0.36	−0.06
8 Nov. -30 Nov.	6.45	5.50	14	45	0.00	0.01	4.01	11.49	2.07	−1.78	0.19	−0.47
Total											14.66	32.45
Mean							4.84	13.33				
1973:												
16 Mar. - 7 Apr.	0.98	1.02	187	185	0.57	0.66	7.14	7.48	14.49	12.70	2.38	2.19
8 Apr. -26 Apr.	1.57	1.48	154	168	1.23	0.15	8.93	9.55	24.36	19.37	4.13	3.51
27 Apr. -18 May	3.33	2.75	109	150	1.74	0.89	12.14	14.42	32.65	27.30	8.72	8.66
19 May - 7 June	4.69	3.63	65	106	2.42	2.26	11.85	15.37	17.65	14.52	4.02	4.24
8 June -27 June	6.92	4.98	41	63	1.09	1.75	10.82	12.33	19.31	15.68	4.16	3.87
28 June -19 July	7.31	5.99	34	45	0.42	0.90	11.00	11.22	2.49	8.37	0.60	2.07
20 July - 9 Aug.	6.87	6.96	32	41	0.30	0.01	10.31	12.07	−2.96	7.13	−0.64	1.81
10 Aug. -30 Aug.	7.00	7.10	30	40	0.15	0.12	9.46	12.78	0.89	0.95	0.18	0.25
31 Aug. -19 Sept.	6.76	7.89	29	37	0.17	0.75	9.07	12.61	−1.66	5.02	−0.32	1.33
20 Sept.-10 Oct.	6.48	8.23	29	33	0.00	0.28	8.73	12.09	−2.01	2.01	−0.37	0.51
11 Oct. -31 Oct.	6.35	9.00	26	29	0.86	0.78	7.58	11.36	−0.97	4.26	−0.15	1.02
1 Nov. -21 Nov.	6.65	8.71	22	25	0.59	0.53	6.50	10.06	2.18	−1.56	0.30	−0.33
22 Nov. -12 Dec.	6.07	8.66	19	23	0.91	0.20	5.49	9.08	−4.34	−0.27	−0.50	−0.05
Total											22.51	29.08
Mean							9.16	11.57				

heated stream was about twice as high in 1973 as in 1972, while average biomasses were slightly reduced following repairs in the control stream. Peak production in both streams occurred from April to June (Table 1, Figure 3), this being related to the high growth rates that took place during spring. Differences in production between the streams, however, were related primarily to higher population biomasses maintained in the control stream than in the heated stream, rather than to differences in growth rate.

Production of salmon in the heated stream during the spring, 1973, was higher than in the spring 1972 (Figure 3). The fish were stocked as fry in 1973, whereas in 1972 they were introduced as eyed eggs. The low average growth rate and survival (Table 1) of fish reared in the heated stream from the egg stage suggest that production was influenced by conditions during early development. Some individuals grew very rapidly during their first few weeks of residence; others apparently did not make the transition to feeding in the heated stream and died from the effects of starvation. Negative production occurred during fall months, when many fish had stopped growing and some were losing weight.

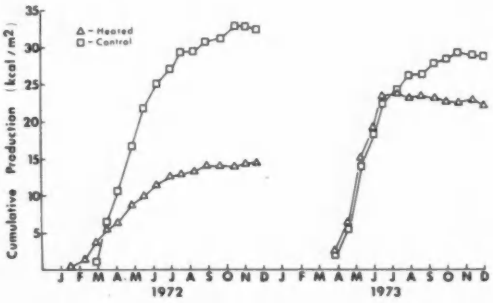

FIGURE 3.—Cumulative production of juvenile chinook salmon during 1972 and 1973.

Direct Temperature Effects on Growth

Relationships between average relative growth rate and food consumption rate of juvenile chinook salmon held in water from the model stream (Figure 4) showed that differences between fish held in heated and unheated water were greatest at low rations and least at high rations. At low rations, control individuals were most efficient; at high levels, there was no appreciable difference except during spring when the elevated temperature facilitated increased food consumption and growth efficiency. The highest rations were close to the maximum amount of food that the young salmon would eat at one feeding in a day, and the graphs for summer and fall indicate that maximum consumption declined as individuals' size increased.

The relationships observed in the experiments between temperature, ration level, and fish size were consistent with the results of laboratory studies of sockeye salmon, *O. nerka* (Brett et al. 1969; Brett and Shelbourn 1975); coho salmon (Averett 1969); and steelhead trout, *Salmo gairdneri*, (Wurtsbaugh 1973). At low levels of food availability, increased metabolic requirements associated with elevated temperature resulted in reduced growth rates; at high levels of food availability, growth rates were not appreciably altered by thermal increases. If responses of juvenile chinook to the range of ration levels in the aquarium growth experiments approximated growth of fish in the model streams at differing consumption rates (Carline and Hall 1973), the growth rate data of Table 1 suggest that during most of the year the fish were feeding well below their maximum possible consumption. Only during certain periods in late winter and spring did growth rates approximate the maximum rates shown in Figure 4. From this we concluded that,

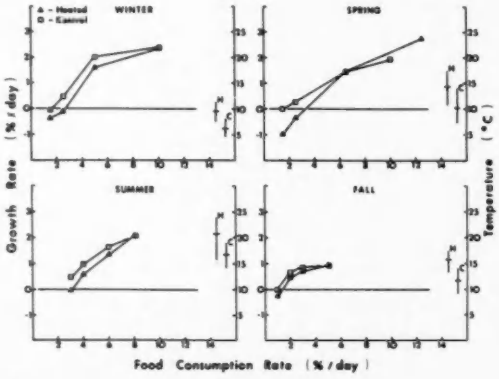

FIGURE 4.—Seasonal changes in the growth rates of juvenile chinook salmon. Experiments continued for 10 days and were preceded by 10 days of acclimation to temperature and ration size. Plotted values of growth rate at each feeding level were based upon the following numbers of fish: winter - 20; spring - 20; summer - 12; and fall - 10. Mean caloric contents (kcal) of the fish at the beginning of each experiment were: winter - 0.59; spring - 1.26; and summer - 7.05; and fall - 8.37.

during most of the year, the experimentally elevated temperature contributed directly to the reduced growth and production of the fish.

Disease

An unexpected indirect effect of elevated temperature was apparent protection from infestation by an intermediate stage of the trematode *Nanophyetus salmincola*, which was present in the streams from late spring through fall. Infective cercaria emerged from the snail *Oxytrema silicula* to encyst in the skin and tissues of juvenile chinook as metacercaria. The distinction between heavy vs. light infestation was made visually and was somewhat arbitrary (Figure 5): conspicuous bumps at the base of the caudal peduncle, darkening of fins, and papules on the body surface were considered symptoms of heavy infestation. While the parasite was obviously present in 1972, it was not until after its appearance in 1973 that attempts were made to quantify its effects.

Infestation rates in the heated stream remained low through summer and early fall and increased until termination of the experiment. Heavy infestations were present in most of the control fish soon after cercaria had begun emerging from the snails. In addition, a greater difference existed between the mean weights of heavily and lightly infested individuals in the control stream than in the heated stream. The impact of this parasite thus appeared to be more severe in the control than in the heated stream.

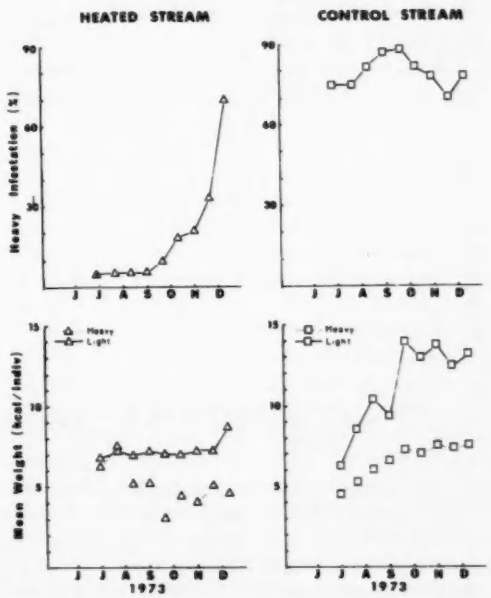

FIGURE 5.–Infestation rates and weight differences of juvenile chinook salmon infested by metacercaria of *Nanophyetus salmincola*.

Food Availability

An understanding of changes in food availability required: 1) that preferred food items be identified, 2) that it be determined when they were available for consumption, and 3) that their relative abundance was estimated under comparable circumstances. In this study, the second requirement was met through observation; food organisms became available only when they entered the drift and then mainly during daylight. Unlike many other salmonids, juvenile spring chinook salmon placed in the model streams were never seen feeding on invertebrates in the benthos. The extent of feeding during darkness was not determined, but was believed to be small. Identical sampling procedures were assumed to fulfill the third requirement, although differential consumption of food before it entered the drift nets could have caused some error.

Oligochaetes were almost completely excluded from the diet of large fish even though they composed an important fraction of the drift (Table 2). Mollusca (exclusively *Gyraulus* sp.) and Trichoptera were comparatively large food items and were consumed more readily by large fish than by small fish. Ostracod *Herpetocypris chevreuxi* was taken throughout the year in proportion to its relative abundance, while Ephemeroptera and Chironomidae–generally small organisms that were usually numerous in the drift–were preferred by smaller fish although these groups were always major components of the diet. In general, differences in food habits between populations in the streams were related to differences in the relative abundance of various food groups. One exception was the greater consumption of terrestrial forms (primarily aphids and spiders) by fish in the heated stream, despite approximately equal input of these invertebrates into both streams.

Measurements of food organisms drifting during daylight hours (Figure 6) were not well correlated with measurements of the biomass of those organisms in the riffle benthos (Figure 7).

TABLE 2.–Average percentages of different taxa (by weight) in the food of juvenile chinook salmon compared with percentages of those organisms in the day drift (in parentheses). H = heated stream, C = control stream.

	Oligochaeta		Mollusca		Ostracoda		Collembola		Ephemeroptera	
Season	H	C	H	C	H	C	H	C	H	C
1972:										
Winter	0(45)	<1(24)	1(4)	0(5)	5(4)	0(0)	1(<1)	0(4)	2(4)	30(2)
Spring	0(43)	0(37)	0(13)	0(4)	18(7)	4(2)	<1(<1)	<1(<1)	11(3)	45(24)
Summer	1(34)	<1(56)	0(5)	0(2)	32(28)	3(3)	<1(1)	0(<1)	10(<1)	10(8)
Fall	<1(7)	0(13)	2(18)	0(4)	7(4)	4(5)	7(1)	4(1)	12(15)	4(6)
1973:										
Spring	13(14)	15(43)	0(6)	<1(<1)	4(7)	1(<1)	<1(<1)	0(<1)	22(11)	25(6)
Summer	6(3)	1(8)	11(7)	1(2)	12(8)	4(11)	<1(<1)	<1(<1)	10(8)	30(18)
Fall	<1(6)	<1(1)	54(33)	4(5)	4(4)	<1(1)	6(2)	4(2)	4(3)	18(19)

	Plecoptera		Trichoptera		Chironomidae		Terrestrials		Miscellaneous	
Season	H	C	H	C	H	C	H	C	H	C
1972:										
Winter	25(9)	52(42)	0(0)	0(0)	51(26)	16(3)	14(10)	2(14)	<1(<1)	<1(<1)
Spring	12(7)	6(3)	3(<1)	5(21)	27(24)	36(6)	27(2)	7(2)	2(<1)	1(<1)
Summer	1(1)	4(<1)	<1(<1)	9(1)	49(65)	67(36)	2(2)	5(8)	2(5)	2(1)
Fall	2(1)	33(13)	21(1)	25(4)	33(39)	27(33)	14(10)	1(18)	<1(4)	1(1)
1973:										
Spring	<1(<1)	1(<1)	9(<1)	3(<1)	44(30)	49(32)	5(23)	2(16)	2(8)	3(1)
Summer	<1(3)	11(2)	11(1)	12(6)	38(65)	26(36)	8(2)	11(16)	2(3)	4(2)
Fall	<1(1)	9(5)	1(4)	33(10)	11(35)	25(55)	20(6)	7(2)	1(6)	1(1)

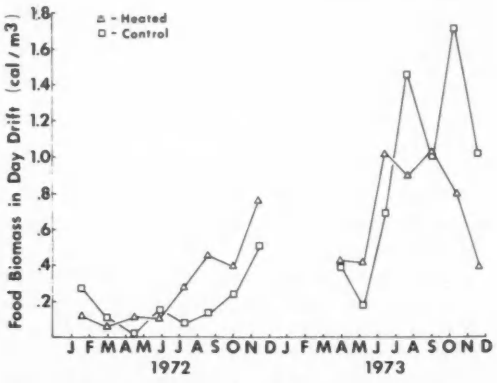

FIGURE 6.–Seasonal changes in the biomass of food organisms present in the day drift. Each point is the mean of two triweekly samples.

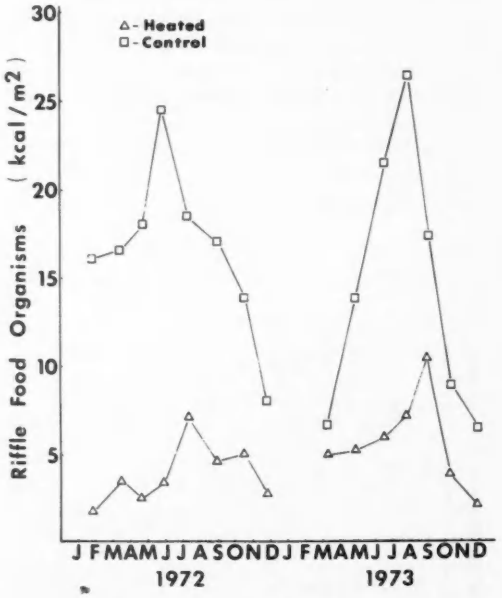

FIGURE 7.–Seasonal changes in the biomass of food organisms present in the riffle benthos. Each point is the mean of two triweekly samples.

Moreover, seasonal patterns in drift differed greatly between 1972 and 1973, with both streams exhibiting higher drift biomasses during the second year than during the first. Although benthic biomasses were significantly greater in the control than in the heated stream, (P<0.001, paired t-test), these differences were often not translated into drift; in fact, during the latter part of 1972 and spring 1973, more food was available in the heated stream. No explanation was found for increased drift in 1973 relative to 1972, but it appeared that increased food availability in 1973 resulted in more growth, higher biomasses, and increased production of fish in the heated stream. Why production in the control stream population did not reflect the greater abundance of food is not

TABLE 3.—Annual average biomasses (cal/m²), drift rates (cal/m³), and drift ratios of selected aquatic taxa, excluding winged adults. Drift ratios were calculated according to the formula (day drift/riffle biomass) × 10^5. Asterisks denote values for the heated stream that were significantly different ($P<0.05$, single classification analysis of variance) from the control.

	1972						1973					
	Heated			Control			Heated			Control		
Taxon	Riffle biomass	Day drift	Drift ratio	Riffle biomass	Day drift	Drift ratio	Riffle biomass	Day drift	Drift ratio	Riffle biomass	Day drift	Drift ratio
Oligochaeta	8,532	0.117	1.74	10,698	0.106	1.43	4,112	0.036	1.26	4,034	0.043	1.56
Mollusca[1]	778	0.031	2.71	127	0.008	6.98	906	0.104	13.18	132	0.029	29.08
Ostracoda	703	0.055	23.63	177	0.010	8.87	273	0.036	29.23	218	0.030	28.40
Ephemeroptera	308	0.024	12.14*	7,812	0.011	0.23	430	0.031	8.46	4,150	0.102	3.12
Plecoptera	378	0.009	7.95*	5,966	0.033	0.59	173	0.002	20.37*	3,717	0.035	1.32
Trichoptera	516	0.001	0.22	1,643	0.018	0.36	570	0.010	5.86	1,569	0.039	2.48
Chironomidae	1,202	0.021	3.26*	1.661	0.011	0.95	2,549	0.052	2.20	1,979	0.045	3.67

[1]*Gyraulus* sp.

known, although severity of infestation by *Nanophyetus* was not compared over the 2 yr and may have been more serious in 1973.

In 1972, drift ratios (the ratio of drift to biomass) of several invertebrate taxa were higher in the heated stream than in the control (Table 3). The next year some of the drift ratios increased, and although many were higher in the control stream, the differences were not statistically significant. Of taxa showing increased drift ratios in the heated stream, Ephemeroptera and Plecoptera were most consistently influenced by elevated temperature. In 1972, Chironomidae also exhibited a significantly greater tendency to drift in the heated stream than in the control. These three groups were important components of both the day drift and the diet of juvenile salmon and often contributed to the greater availability of food in the heated stream than in the control during certain periods.

Fewer macroinvertebrate taxa were present in the heated stream than in the control. Paired *t*-tests indicated that number of taxa were significantly different in both riffles (treatment mean = 21, control mean = 34; $P<0.001$) and pools (treatment mean = 16, control mean = 19, $P<0.01$). Most of those taxa that were unique to one stream or the other were very rare and contributed little to fish production. Major biomass differences arose because many taxa had greater population densities in the control while only a few fared better in the heated stream. The several taxa that did exhibit higher biomass in the heated stream were very abundant and tended to dominate the bottom fauna to a greater extent than did common taxa in the control. The two most abundant invertebrates in the heated stream were *Oxytrema silicula* in the riffles and *Limnodrilus* sp. in the pools. Neither of these two species was consumed in significant quantities by the young salmon; thus, increased dominance in the heated stream did not give rise to greater food availability.

Periphyton Biomass and Sedimentation

Plants and detritus were significantly more abundant in the heated stream ($P<0.001$, paired *t*-test) than in the control (Figure 8). The greater amounts of plants and detritus in the heated

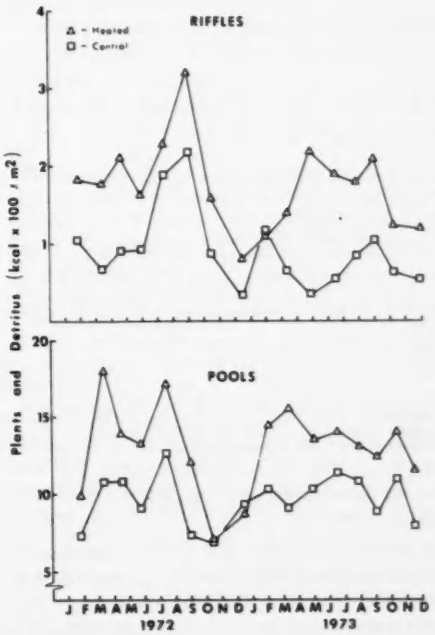

FIGURE 8.—Biomasses of plants and detritus in riffles and pools of the model streams. Each point is the mean of two triweekly samples.

stream than in the control were due to the high densities of filamentous algae in the riffles and the considerable accumulation of organic detritus in the pools. Increased primary production associated with elevated temperature in laboratory streams has been measured by Kevern and Ball (1965) and Phinney and McIntire (1965). The dominant algal species in our model streams, *Cladophora glomerata*, grows rapidly at high temperatures (Whitton 1971; Adams and Stone 1973).

Heavy growths of algae on the riffles apparently accelerated sedimentation rates in the heated stream (Table 4) by acting as filters to trap and consolidate fine particles introduced with exchange water. In the pools, where filamentous algae did not grow, fine sediment levels in both streams were similar. By indirectly enhancing sediment accumulation, elevated temperature probably had an important effect on the numbers of food organisms available to salmon in the heated stream. Hynes (1960) described how siltation alters the habitat of many invertebrates, with the result usually being a reduction in benthic biomass (Cordone and Kelly 1961). Greatly reduced mean annual biomasses of Ephemeroptera, Plecoptera, and Trichoptera in the heated stream (Table 3) compared with the control suggest that these groups were influenced by the amount of fine sediments in the substrate, and these insects were often preferred food items of the fish (Table 2).

TABLE 4.–Levels of fine sediments, expressed as grams dry weight per square meter, in the model streams during May 1974. The figures in parentheses refer to the amount of time that had elapsed since a major disturbance to the riffles.

Item	Particle size (mm)		
	0.175-1	0.088-0.175	0.088
Riffles:			
Control (17 mo)	41	19	169
Heated (17 mo)	147	37	943
Heated (31 mo)	167	91	1,443
Pools:			
Control	94	1,219	1,746
Heated	86	1,064	1,728

DISCUSSION

Our study was designed to examine the effects of elevated temperature on the production of juvenile chinook salmon. The constantly elevated temperature was not meant to simulate a particular type of thermal increase, but was within the range of temperature elevations caused by heated discharges into running waters (Wilber 1969, Parker and Krenkel 1970), irrigation runoff (Eldridge 1963), and removal of streamside vegetation (Brown and Krygier 1970). It was also within the limits of temperature increase legally allowed by some regulations (Burd 1969).

Both direct and indirect temperature effects influenced chinook salmon production, but the magnitude of these effects varied seasonally. Production was high in spring because temperature was in a range that was favorable to growth, parasitism had not yet become an important factor, and the small fish were able to efficiently exploit available food. Summer was generally a period of declining production because high temperatures resulted in an increase in maintenance requirements and, for the control stream, because parasites had attacked the majority of the population. Low production during late summer and fall was associated with high levels of infestation and the ineffectiveness of large fish in exploiting small organisms that were abundant in the drift.

The lack of correlation that existed between growth rates (Table 1) and food availability (Figure 6) may have been related to the species composition of drifting invertebrates. A high percentage of summer and fall drift was composed of very small forms such as oligochaetes (*Nais communis*) and chironomids (Table 2). During those seasons, tiny organisms were not preferred food items of the young salmon, which were larger and less numerous than during the spring. High growth rates exhibited by fish during winter and spring when drift rates were comparatively low suggest that smaller, more abundant fish were able to utilize the entire range of sizes of invertebrate species that left the substrate. It was impossible to determine whether food size preference affected fish in the two streams identically, but based on overall invertebrate composition (Table 3), taxa containing species of large size (Ephemeroptera, Plecoptera, Trichoptera) were more abundant in the control than in the heated stream. This was reflected in higher growth rates of salmon in the control than in the heated stream during summer and fall. Clearly, more intensive examination of the relationship between prey size and prey selection by salmonids is needed.

Low benthic invertebrate biomasses in the heated stream were associated with increased sedimentation rates and reduced numbers of taxa. Iverson (1972) suggested that the poor success of certain invertebrates in the heated stream was

due to their being cold-adapted species. No large scale mortality of larvae or pupae was detected in the heated stream, even during summer months. However, very early developmental stages and life history patterns may have been altered (Macan 1961a, b; Hynes 1970).

The tendency of certain invertebrates in the heated stream to enter the drift in greater proportion to their benthic biomasses (Table 3) was probably related both to elevated temperature and to fine sediment levels. Increased drift associated with increasing temperature was described for certain invertebrates by Müller (1963), Waters (1968), and Pearson and Franklin (1968). In other studies, significant positive correlations between drift and temperature have not been detected (Bishop and Hynes 1969; Wojtalik and Waters 1970; Müller 1970; Reisen and Prins 1972). Experimental additions of sediments to a stream were found by Rosenberg and Weins (1975) to significantly increase the drift of some invertebrate taxa and to have inconsistent effects on others.

Although the influence of elevated temperature on the production of juvenile chinook salmon was complex, we were able to identify both beneficial and harmful effects. The fish benefited in several ways. First, the temperature increase may have stimulated higher consumption rates when suitable food was very abundant, although this condition was rarely achieved. Second, higher temperatures afforded protection from infestation by a trematode parasite, which heavily infested the majority of individuals in the control stream. Third, certain invertebrates may have been stimulated to enter the drift and thus became more available as food. Fish were harmed in at least two ways. First, growth efficiencies were lowered at all but the highest consumption levels. Second, despite high drift ratios of some taxa, food availability was generally reduced because preferred food organisms were much less abundant in the substrate of the heated stream than in the control. The net result was that salmon production in the heated stream was about 50% less in 1972 and 25% less in 1973 compared with the unheated stream.

ACKNOWLEDGMENTS

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LITERATURE CITED

ADAMS, M. S., AND W. STONE.
1973. Field studies on photosynthesis of *Cladophora glomerata* (Chlorophyta) in Green Bay, Lake Michigan. Ecology 54:853-862.

ANDERSON, N. H.
1967. Biology and downstream drift of some Oregon Trichoptera. Can. Entomol. 99:507-521.

AVERETT, R. C.
1969. Influence of temperature on energy and material utilization by juvenile coho salmon. Ph.D. Thesis, Oregon State Univ., Corvallis, 75 p.

BISHOP, J. E., AND H. B. N. HYNES.
1969. Downstream drift of the invertebrate fauna in a stream ecosystem. Arch Hydrobiol. 66:56-90.

BRETT, J. R., AND J. E. SHELBOURN.
1975. Growth rate of young sockeye salmon, *Oncorhynchus nerka*, in relation to fish size and ration level. J. Fish. Res. Board Can. 32:2103-2110.

BRETT, J. R., J. E. SHELBOURN, AND C. T. SHOOP.
1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. 26:2363-2394.

BROWN, G. W., AND J. T. KRYGIER.
1970. Effects of clear-cutting on stream temperature. Water Resour. Res. 6:1133-1139.

BURD, R. S.
1969. Water quality standards for temperature. *In* F. L. Parker and P. A. Krenkel (editor), Engineering aspects of thermal pollution, p. 72-77. Vanderbilt Univ. Press, Nashville.

CARLINE, R. F., AND J. D. HALL.
1973. Evaluation of a method for estimating food consumption rates of fish. J. Fish. Res. Board Can. 30:623-629.

CORDONE, A. J., AND D. W. KELLEY.
1961. The influences of inorganic sediment on the aquatic life of streams. Calif. Fish Game 47:189-228.

CUMMINS, K. W.
1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. Am. Midl. Nat. 67:477-504.

CUMMINS, K. W., AND J. C. WUYCHECK.
1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Theor. Angew. Limnol. 18:1-158.

ELDRIDGE, E. F.
1963. Irrigation as a source of water pollution. J. Water Pollut. Control. Fed. 35:614-625.

HYNES, H. B. N.
1960. The biology of polluted waters. Liverpool Univ. Press, Liverpool, 202 p.
1970. The ecology of running waters. Univ. Toronto Press, Toronto, 555 p.

IVERSON, R. A.
1972. Effects of elevated temperature on juvenile coho salmon and benthic invertebrates in model stream communities. Ph.D. Thesis, Oregon State Univ., Corvallis, 98 p.

KEVERN, N. R., AND R. C. BALL.
1965. Primary productivity and energy relationships in artificial streams. Limnol. Oceanogr. 10:74-87.

MACAN, T. T.
1961a. Factors that limit the range of freshwater animals. Biol. Rev. (Camb.) 36:151-198.
1961b. A review of running water studies. Int. Ver. Theor. Angew. Limnol. Verh. 14:587-602.

MÜLLER, K.
1963. Diurnal rhythm in organic drift of *Gammarus pulex*. Nature (Lond.) 198:806-807.
1970. Die Drift von Insektenlarven in Nord - und Mitteleuropa. Österr. Fisch. 23:111-117.

PARKER, F. L., AND P. A. KRENKEL.
1970. Physical and engineering aspects of thermal pollution. CRC Press, Cleveland, 100 p.

PEARSON, W. D., AND D. R. FRANKLIN.
1968. Some factors affecting drift rates of *Baetis* and Simuliidae in a large river. Ecology 49:75-81.

PHINNEY, H. K., AND C. D. MCINTIRE.
1965. Effect of temperature on metabolism of periphyton communities developed in laboratory streams. Limnol. Oceanogr. 10:341-344.

REISEN, W. K., AND R. PRINS.
1972. Some ecological relationships of the invertebrate drift in Praters Creek, Pickens County, South Carolina. Ecology 53:876-884.

ROSENBERG, D. M., AND A. P. WEINS.
1975. Experimental sediment addition studies on the Harris River, N.W.T., Canada: the effect on macro-invertebrate drift. Int. Ver. Theor. Angew. Limnol. Verh. 19:1568-1574.

WARREN, C. E.
1971. Biology and water pollution control. W. B. Saunders Co., Phila., 434 p.

WARREN, C. E., J. H. WALES, G. E. DAVIS, AND P. DOUDOROFF.
1964. Trout production in an experimental stream enriched with sucrose. J. Wildl. Manage. 28:617-660.

WATERS, T. F.
1968. Diurnal periodicity in the drift of a day-active stream invertebrate. Ecology 49:152-153.

WHITTON, B. A.
1971. Terrestrial and freshwater algae of Aldabra. Philos. Trans. R. Soc. Lond., Ser. B., Biol. Sci. 260:249-255.

WILBER, C. G.
1969. The biological aspects of water pollution. Charles C. Thomas, Springfield, Ill., 296 p.

WOJTALIK, T. A., AND T. F. WATERS.
1970. Some effects of heated water on the drift of two species of stream invertebrates. Trans. Am. Fish. Soc. 99:782-788.

WURTSBAUGH, W. A.
1973. Effects of temperature, ration, and size on the growth of juvenile steelhead trout, *Salmo gairdneri*. M.S. Thesis, Oregon State Univ., Corvallis, 69 p.

REPRODUCTIVE CYCLE, FECUNDITY, AND SEX RATIOS OF THE RED PORGY, *PAGRUS PAGRUS* (PISCES: SPARIDAE) IN NORTH CAROLINA

CHARLES S. MANOOCH, III[1]

ABSTRACT

Macroscopic examination of gonads and gonad indices demonstrated that March and April were the peak spawning months in Raleigh and Onslow bays, N.C. Ripe fish were collected over irregular bottom from January to April in water ranging from 21 to 100 m in depth. Bottom temperatures during the spawning period ranged from 16.4° to 21.5°C. Three predictors of fecundity, total length, weight, and age were evaluated and regression equations derived. Fish weight proved to be the most precise predictor of fecundity: ln fecundity = 1.7369 + 1.5178 (ln weight of the fish) where fecundity is the total number of eggs in both ovaries. Fecundity estimates ranged from 48,660 for a 304-mm (390-g) red porgy to 488,600 for a 516-mm (1,783-g) fish. Although some individuals reached sexual maturity at age II, most spawn for the first time at age III. Chi-square tests revealed a significant departure from the expected 1:1 sex ratio when data were stratified by month, year, and size. Females were encountered more frequently each month for all 3 yr, and in the smaller size intervals.

The red porgy, *Pagrus pagrus* Linnaeus, is one of the most important demersal marine fishes taken by recreational anglers fishing from headboats[2] between Cape Hatteras, N.C., and Charleston, S.C. In 1972 and 1973, 513,700 red porgy weighing 1.3 million pounds were taken by this sport fishery (Sekavec and Huntsman 1972; Huntsman 1976). In spite of the importance of the species, published information on the red porgy in the western Atlantic is scarce. Dias et al. (1972) described the length-weight relationship for *Pagrus* collected off South Carolina; Ciechomski and Weiss (1973) reported on egg, embryo, and larval development of red porgy from the Argentine Sea; and Manooch et al. (in press); Manooch (in press), discussed the taxonomic status and the food habits of *P. pagrus*, respectively.

This study investigated reproduction of red porgy in North Carolina to determine: 1) spawning season, 2) size and age of females at sexual maturity, 3) prediction equations for estimating fecundity, 4) sex ratios by month and size, 5) spawning ecology, and 6) a description of the eggs and young. This research is part of a National Marine Fisheries Service project which is studying the bottom fishes of the outer continental shelf of the Carolinas.

MATERIALS AND METHODS

Length, weight, sex, stage of gonad development, and gonad length and weight were recorded for fish sampled from North Carolina headboats and by experimental fishing aboard the RV *Onslow Bay* from 1972 to 1974. Gonads were preserved in 10% Formalin[3] and macroscopically examined to determine maturity using modified criteria from Orange (1961): Stage 1-S: infantile, gonads small and ribbonlike (sex determination by gross examination not possible); Stage 1: immature, gonads elongated, slender, but sex discernible by gross examination; Stage 2: early maturing, gonads slightly enlarged, individual ova not visible to naked eye; Stage 3: late maturing, gonads enlarged, individual ova visible to naked eye; Stage 4: ripe, ovary greatly enlarged, many ova translucent and easily dislodged from follicles or loose in lumen of ovary; and Stage 5: spawned, includes recently spawned fish with mature ova occurring as remnants in various stages of reabsorption.

Time of spawning based on 243 females was determined by using: 1) the gonad index (G.I.) of Schaefer and Orange (1956), and 2) the index: 100G.W./F.W., where G.W. is the fresh gonad weight to the nearest 0.01 g and F.W. is the body weight of the fish to the nearest 1.0 g. Mean values

[1]Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

[2]Headboats are those that charge for a day's fishing on a per person basis.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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of these indices were plotted monthly, to thus indicate duration and peak of spawning, and age and size at sexual maturity. The linear regressions fecundity on length, weight, and age were calculated based on mature (Stage 4) ovaries from 50 females (ages II-IX, 304 to 520 mm TL) collected from January through March for the years 1973 and 1974. One ovary randomly selected from each pair was blotted dry and weighed to the nearest 0.01 g. The selected ovary was crumbled and all ovarian tissue removed. The eggs were then filtered, blotted dry, and weighed. One sample from each ovary of 0.2-0.4 g was weighed to the nearest 0.001 g and placed in a 6 × 6 counting grid and all ova were counted. The formula:

$$Y = \frac{(W)(W_i')}{(W_i)(w)} \quad y$$

was used to estimate the number of eggs in the ovaries, where Y = total number of eggs in both ovaries, W = weight of both ovaries, W_i = weight of selected ovary, W_i' = weight of ovary after removal of ovarian tissue, w = weight of sample, and y = number of eggs in the sample (Lassiter 1962).

RESULTS AND DISCUSSION

Sexual Maturity

Ovary condition progressed from ripe, Stage 4, dominant from January through March, to spawned, Stage 5, dominant from May through June, indicating that peak spawning occurred in March and April (Figure 1). Ovaries collected in April and May were flaccid and showed resorption of eggs. By June all of the fish were early maturing. The ovaries gradually became more firm after resorption in early summer and little change in gonad condition was noted in late summer and early fall. Maturation of ovaries occurred between October and January. Stratification of the sexual maturity data by month supported the hypothesis of late winter to early spring spawning. Approximately 23% of the fish examined in January were late maturing and 77% were ripe. By February, 12.5% were classified as late maturing, and 87.5% were ripe. The first spawned (Stage 5) fish were collected in March and their frequency of occurrence increased to 60.5% in April (Figure 2). Walker (1950) reported ripe *P. pagrus* in January and February off North Carolina, and Ranzi (1969) found that they were sexually mature from April to June in the Mediterranean Sea off Algeria.

Early maturing and ripe stages of males were easily discernible by gross examination of the testes, but the late maturing and ripe classes were difficult to separate. Milt could be pressed from the

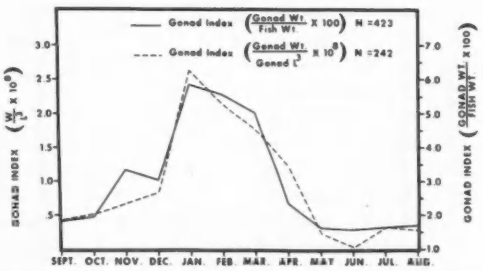
Gonad Index (Gonad Wt. / Fish Wt. × 100) N =423
Gonad Index (Gonad Wt. / Gonad L³ × 10⁶) N =242
GONAD INDEX (Gonad Wt. / Gonad L³ × 10⁶)
GONAD INDEX (GONAD WT. / FISH WT. × 100)
SEPT. OCT. NOV. DEC. JAN. FEB. MAR. APR. MAY JUN. JUL. AUG.

FIGURE 1.–Mean monthly gonad indices for female *Pagrus pagrus* collected from Onslow Bay, N.C., 1972 to 1974.

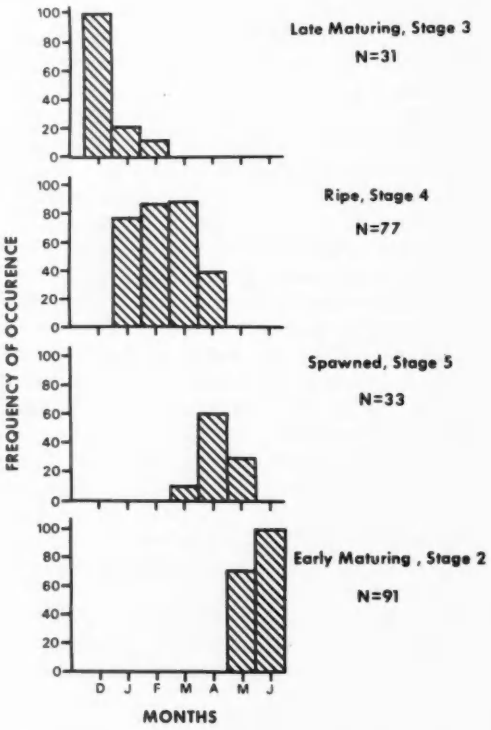

FIGURE 2.–Percentage of female red porgy at various stages of sexual maturity, collected in Onslow and Raleigh bays, N.C., by month.

central canal of testes from January through April.

Female red porgy were separated into two maturity classes: Immature fish, and mature (maturing, ripe, and spawned). No individuals less than 260 mm and all fish greater than 360 mm were sexually mature (Table 1). The linear regression of percent maturity (Y) on total length (X):

$$Y = -211.2946 + 0.8576X, r = 0.94,$$

was significant at $\alpha = 0.01$. Half the females were mature at 304 mm. By inserting age data (Manooch 1975) to the graph, age at sexual maturity was determined. Regression of age with length suggests that none of the age I fish, 37% of the age II, 81% of the age III, and 100% of the age IV fish were mature. Some age II and III females apparently showed the characteristic, seasonal maturation of ovaries but did not spawn the first year, because several specimens had ovaries containing absorbed ova during the peak spawning period.

TABLE 1.–Number and percentage of female red porgy, grouped into 20-mm size categories, staged as immature and mature (maturing, ripe, and spawned) off North Carolina 1972-74.

Total length (mm)	Immature (no.)	Mature (no.)	Mature (%)
<220	22	0	0.0
220-239	1	0	0.0
240-259	4	0	0.0
260-279	8	4	33.3
280-299	11	2	15.4
300-319	5	7	58.3
320-339	4	29	87.9
340-359	5	34	87.2
360-379	0	57	100.0
380-399	0	80	100.0
400-419	0	75	100.0
420-600	0	214	100.0
Total	60	502	

Fecundity

Regression analyses indicated total length, weight, or age could be used to predict fecundity of red porgy, but weight proved to be the best predictor of fecundity ($r^2 = 0.70$) and had the lowest error mean square. Combinations of two independent variables, weight and length, improved predictability only slightly, therefore, separate equations were derived by using weight on fecundity, and length on fecundity. The equations describing the relationships (Figure 3) and coefficients of determination (r^2) are:

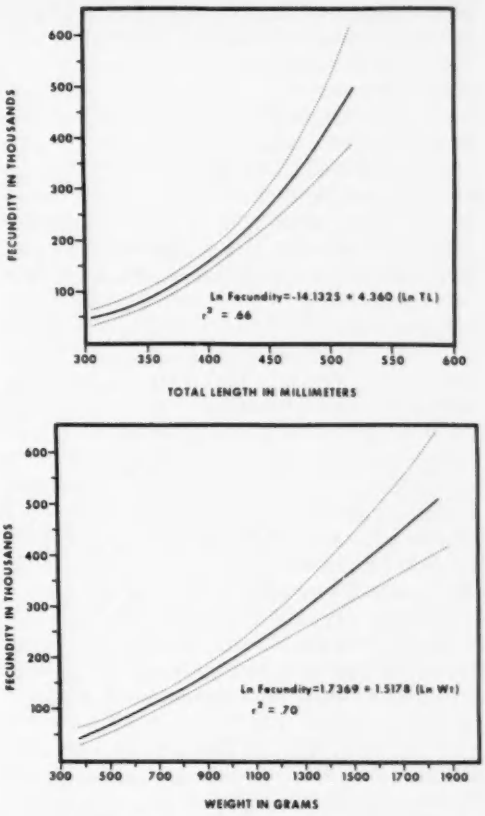

FIGURE 3.–Relationship between fecundity and two predictors: (top) length and (bottom) weight of 50 red porgy collected in Onslow Bay, N.C.

$$\ln \text{Fecundity} = 1.7369 + 1.5178(\ln \text{Wt}), \quad r^2 = 0.70 \text{ and}$$

$$\ln \text{Fecundity} = -14.1325 + 4.3598(\ln \text{TL}), \quad r^2 = 0.66.$$

The 95% confidence limits have also been calculated. Predicted fecundity ranges from 48,660 eggs for fish 304 mm TL and 390 g in weight to 488,600 ova for fish 516 mm TL and 1,783 g. Theoretically, a 600-mm red porgy which is not uncommon in the sport catch, could produce approximately 943,000 eggs if maximum ova production is not obtained at a smaller size.

Sex Ratios and Hermaphroditism

Sex of 736 red porgy collected in 1972, 1973, and 1974 was grouped by year and month, and data

revealed females to be more abundant in the catch than males (Table 2). The sex ratio was not 1:1 males to females as hypothesized but actually 1:2.1 when the years were combined. Data for each year analyzed separately also provided significant deviations from expected. The sex ratio for each year was 1:2.1, 1:1.9, and 1:3.3 for 1972, 1973, and 1974, respectively (Table 2). The overall, higher deviation from 1:1 for 1974 is because most of the fish were collected in late winter and spring of that year, months which reflected the greatest deviation from 1:1. Of all months examined, only August, September, and November were nonsignificant, revealing equal number of males and females. The ratio for October could not be tested because of insufficient data. During the spawning season, chi-square values were very high and perhaps reflect monosexual schooling.

Sex ratios for males and females grouped into 50-mm length intervals had significant departures from the expected 1:1 ratio for most size categories (Table 3). In general, females predominated in the smaller size classes, whereas males predominated in the larger size classes. The nonsignificant value for the smallest size interval is probably unrealistic since the sample is very small and the sequential intervals are highly significant in favor of females.

Both protandrous and protogynous hermaphroditism are relatively common among the sparids (D'Ancona 1950, 1956). *Pagrus pagrus* collected from the west coast of Florida appear to display protogynous hermaphroditism although data available are insufficient for quantitative description (D. S. Beaumariage pers. commun.).

TABLE 2.–Number of male and female red porgy collected by month during 1972, 1973, and 1974 with chi-square values obtained from testing a 1:1 sex ratio in each month (a), and each year (b).

Month	Year 1972	1973	1974	Total[a]	df	X^2
May	9:12	17:41	0:5	26:58	2	12.08**
June	16:22	26:45	—	42:67	1	5.74*
July	9:27	27:44	—	36:71	1	11.44**
Aug.	11:15	30:33	—	41:48	1	.55
Sept.	3:9	21:26	—	24:35	1	2.04
Oct.	1:9	—	—	1:9		
Nov.	2:3	12:15	—	14:18	1	.50
Dec.	5:15	3:11	—	8:26	1	9.52**
Jan.	—	0:2	9:22	9:24	1	6.82**
Feb.	—	5:12	8:32	13:44	1	16.86**
Mar.	—	5:26	4:32	9:58	1	17.92**
Apr.	—	6:29	10:10	16:39	1	9.62**
Total[b]	56:112	152:284	31:101	239:497		
df	7	10	4	11		
X^2	18.6**	39.96**	37.12**	90.44**		

* = $P < 0.05$.
** = $P < 0.01$.

TABLE 3.–Number of male and female red porgy grouped into 50-mm size categories with chi-square values assuming a 1:1 sex ratio.

Length	Male	Female	Total	X^2
<300	1	6	7	3.57
300-350	2	53	55	47.28**
351-400	10	157	167	129.40**
401-450	48	161	209	61.10**
451-500	124	83	207	8.12**
501-550	51	27	78	7.38**
551-600	3	10	13	3.76
>600	1	0	1	—
Totals	240	497	737	

* = $P < 0.05$.
** = $P < 0.01$.

The predominance of females at smaller size intervals in this study and discovery of individuals with both ovarian and testicular tissue supports the theory of protogyny. Although hermaphroditic red porgy were found by macroscopic examination, only 16 specimens of the 752 examined (2%) contained both male and female gonadal tissues. Hermaphroditic red porgy ranged in size from 325 mm to 424 mm TL ($\bar{x}$ = 400 mm); possibly the length range over which sexual transition takes place. In each fish the ovaries were dominant with only redundant testicular tissue present. From preliminary studies with red porgy in the Gulf, M. A. Moe (pers. commun.) reported that the male portion of the gonad develops in the muscular tunica of the gonad wall and eventually completely takes over the gonad.

Spawning

Ripe red porgy were collected over irregular bottom from January through April in water depth ranging from 21 to 100 m and bottom temperatures of 16.4° to 21.5°C (Figure 4). *Pagrus pagrus* spawns from December through January in the Argentine Sea when water temperature is approximately 20° to 21°C (Ciechomski and Weiss 1973).

The relationship of the gonad index to photoperiod and bottom temperature were plotted monthly (Figure 4). By inspecting this figure one could conclude that photoperiod is more directly correlated to gonad maturation and spawning. Similarly, gonad maturation of red grouper, *Epinephelus morio*, another demersal reef species, was unrelated to bottom temperature (Moe 1969). Harrington (1956) demonstrated the importance of photoperiod to gonad maturation and spawning

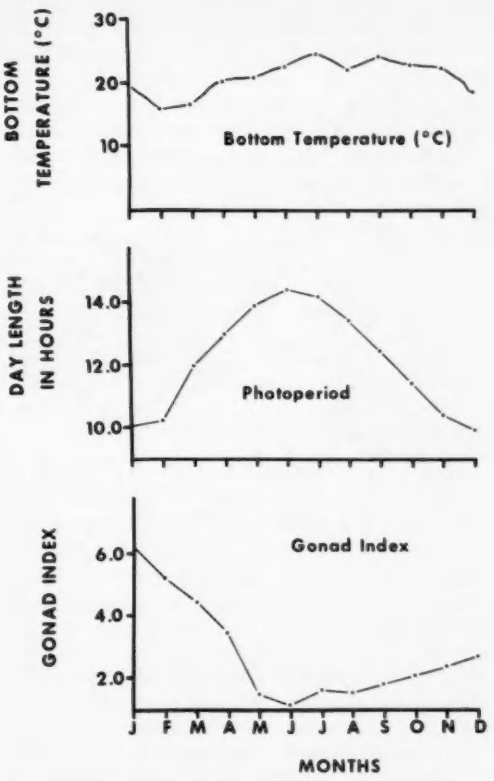

FIGURE 4.—Mean gonad indices for female *Pagrus pagrus* for each month compared with photoperiod and bottom temperatures.

for the banded sunfish, *Enneacanthus obesus*. *Pagrus pagrus* spawns between January and April, when photoperiod increases rapidly, but when bottom temperatures fluctuate irregularly. Gonads were in spent and resting stages during maximum photoperiod, May to August, and began developing as photoperiod decreased. The graphs suggest that seasonal increase in photoperiod in late winter and early spring initiates final maturation of ovaries and ultimately, the spawning of *P. pagrus*.

Eggs and Young

Red porgy eggs are pelagic, spherical, without appendages and contain a single oil droplet. Preserved eggs were generally yellow to orange in color, they measured 0.31 to 0.94 mm in diameter and the oil droplet was 0.20 to 0.32 mm in diameter. This size description is similar to the unfertilized eggs of another sparid, *Stenotomus chrysops*, which were 0.66 to 0.95 mm and had an oil droplet 0.17 to 0.40 mm in diameter (Finkelstein 1969). I induced three females (355-560 mm TL) to release ova in aquaria in March 1975. These eggs appeared transparent and were noticeably larger than those described above. Since I considered these eggs to be most representative of mature, unfertilized eggs, I recorded size for 10 eggs from each fish. Their mean size was 0.88 mm in diameter and ranged from 0.64 to 0.92 mm; the oil droplet averaged 0.25 mm in diameter. Very little difference was found in egg size for each fish.

Prejuvenile red porgy were collected in April off South Carolina. An 18-mm specimen had minute spines along the dorsal and ventral outlines of the body, and five to six vertical pigment bands (Figure 5). These bars appeared red on stressed adults. Ranzi (1969) described young *P. pagrus* from the Bay of Naples and referred to the vertical bands in specimens 13 mm and larger.

Forty-four juvenile *P. pagrus* ranging in length from 42 to 59 mm ($\bar{X}$ = 51 mm) were collected by trawl off Charleston in relatively shallow water (9-20 m); bottom temperatures ranged from 17.5° to 18.5°C. The fish were also collected in April, indicating spawning may occur slightly earlier in that area compared with Onslow Bay and Raleigh Bay, N.C.

SUMMARY AND CONCLUSIONS

Red porgy spawn in North Carolina waters from January through April with a peak in spawning activity between March and April. Maturation of gonads and spawning appear to be correlated with increased photoperiod. Spawning fish were collected over irregular bottom ranging from 21 to 100 m in depth. Bottom temperatures at these depths ranged from 16.4° to 21.5°C. Collection of relatively large juveniles off Charleston in April indicates that spawning may occur earlier there.

Some female *P. pagrus* attain sexual maturity as 2-yr-old fish; however, the majority mature at 3 yr. All of the fish examined had reached sexual maturity by the fourth year. Approximately 50% of the females were mature at 304 mm TL, and 75% were mature at 334 mm. All fish 364 mm or more in length were sexually mature. Evidently, some of the age II and III fish experience regular, seasonal maturation of gonads but do not spawn that first year. This conclusion is based upon several fish I

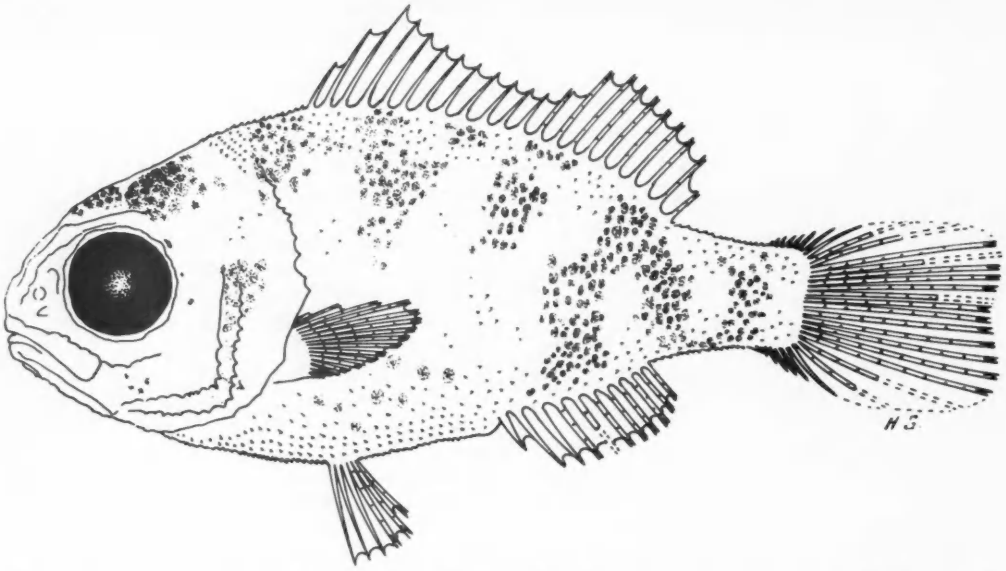

FIGURE 5.—Young red porgy, 18 mm total length, collected by trawl off Charleston, S.C., in April 1974 (drawing by Herbert Gordy, National Marine Fisheries Service, NOAA).

observed which had ovaries containing absorbed ova during the peak spawning period.

Fecundity estimation for red porgy ranged from 48,656 eggs for a 304-mm female to 488,600 ova for a 516-mm fish. Larger fish (>600 mm TL), which occasionally appear in the sport fishery, may produce over 900,000 eggs. Eggs removed from ripe females ranged in size from 0.31 to 0.94 mm in diameter. The developed *P. pagrus* eggs averaged 0.88 mm in diameter and contained a single oil droplet averaging 0.25 mm in diameter. While fecundity was correlated to three predictors; length, weight, and age, weight was the most accurate predictor of fecundity. Although age was not as satisfactory a predictor of fecundity as weight and length, it should not be overlooked, because the age-fecundity relation can have useful application in population modeling. High variability in fecundity estimates for age-groups is expected due to range in size and variation in gonad size among fish of the same size (Bagenal 1967).

Sex ratios for red porgy were usually unbalanced in favor of females. Analyzing data by month, year, and size, I observed a domination by females. The overall sex ratio observed was 1:2. The occurrence of females was higher during the spawning season. This predominance may be attributed to difference in feeding behavior of ripe fish, or to true population differences in the areas sampled. I do not believe gear selectivity influenced sex ratios. The dominance of females for the smaller size classes and actual documentation of hermaphroditic red porgy in the study lends some support to the theory of protogynous hermaphroditism reported for the species in the Gulf of Mexico (Beaumariage pers. commun.). Both protandrous and protogynous hermaphroditism are relatively common among the sparids (D'Ancona 1950, 1956). Although only 2% of the fish examined were obviously hermaphroditic, a complete histological study of gonadal development is needed to determine if the species displays sex reversal. Protogynous hermaphroditism may have selective advantages as Atz (1964:224) mentioned providing an endocrinologically better balanced fish, assuring presence of both sexes in isolated, insular areas, or a mechanism of population control. For the latter purpose, certain population pressures presumably stimulate sexual transition. Probably more applicable to red porgy hermaphroditism is the "size advantage model" proposed by Ghiselin (1969). The theory explains sequential hermaphroditism as occurring when an organism reproduces more efficiently as one sex when small and the opposite sex when larger. A male's poten-

tial, theoretically, is higher than a female's at larger sizes, and conversely, a female's reproductive potential is higher than a male's at smaller sizes. The female reproductive capabilities could continue to increase with age. Perhaps males function more efficiently at larger sizes because they can mate with numerous females. Evolutionary factors which favor protogyny are those which tend to depress male reproductive potential at early ages, such as inexperience, territoriality, or female mate selection (Warner 1975). Without additional information on the spawning behavior of *Pagrus*, it would be difficult to eliminate any of these factors.

ACKNOWLEDGMENTS

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LITERATURE CITED

ATZ, J. W.
1964. Intersexuality in fishes. *In* C. N. Armstrong and A. J. Marshall (editors), Intersexuality in vertebrates including man, p. 145-232. Academic Press, N.Y.

BAGENAL, T. B.
1967. A short review of fish fecundity. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 89-111. Wiley, N.Y.

CIECHOMSKI, J. D. DE, AND G. WEISS.
1973. Desove y desarollo embrionario y larval de besugo, *Pagrus pagrus* (Linné) en el Mar Argentina (Pisces, Sparidae). Physis Rev. Asoc. Argent. Cienc. Nat., Secc. A 32:481-487.

D'ANCONA, U.
1950. Détermination e différenciation du sexe chez les poissons. Arch. Anat. Microsc. Morphol. Exp. 39:274-294.
1956. Inversion spontanées et expérimentales dans les gonades des Téléostéens. Annee Biol., Sér. 3, 32:89-99.

DIAS, R. K., J. K. DIAS, AND W. D. ANDERSON, JR.
1972. Relationships of lengths (standard, fork and total) and lengths to weight in the red porgy, *Pagrus sedecim* (Perciformes, Sparidae), caught off South Carolina. Trans. Am. Fish. Soc. 101:503-506.

FINKELSTEIN, S. L.
1969. Age at maturity of scup from New York waters. N.Y. Fish Game J. 16:224-237.

GHISELIN, M. T.
1969. The evolution of hermaphroditism among animals. Q. Rev. Biol. 44:189-208.

HARRINGTON, R. W., JR.
1956. An experiment on the effects of contrasting daily photoperiods on gametogenesis and reproduction in the centrarchid fish, *Enneacanthus obesus* (Girard). J. Exp. Zool. 131:203-223.

HUNTSMAN, G. R.
1976. Offshore headboat fishing in North Carolina and South Carolina. Mar. Fish. Rev. 38(3):13-23.

LASSITER, R. R.
1962. Life history aspects of the bluefish, *Pomatomus salatrix* (Linnaeus), from the coast of North Carolina. M.S. Thesis, North Carolina State Univ., Raleigh, 68 p.

MANOOCH, C. S.
1975. A study of the taxonomy, exploitation, life history, ecology and tagging of the red porgy, *Pagrus pagrus* Linnaeus off the Carolinas. Ph.D. Thesis, North Carolina State Univ., Raleigh, 275 p.
In press. Food habits of the red porgy, *Pagrus pagrus* Linnaeus (Pisces: Sparidae) off North Carolina and South Carolina, U.S.A. Bull. Mar. Sci.

MANOOCH, C. S., G. R. HUNTSMAN, B. SULLIVAN, AND J. ELLIOTT.
In press. Conspecific status of the sparid fishes *Pagrus sedecim* Ginsberg and *Pagrus pagrus* Linnaeus. Copeia.

MOE, M. A., JR.
1969. Biology of the red grouper, *Epinephelus morio* (Valenciennes), from the eastern Gulf of Mexico. Fla. Dep. Nat. Resour., Mar. Res. Lab., Prof. Pap. Ser. 10, 95 p.

ORANGE, C. J.
1961. Spawning of yellowfin tuna and skipjack in the eastern tropical Pacific, as inferred from studies on gonad development. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 5:457-526.

RANZI, S.
1969. Sparidae. *In* S. Lo Bianco, Eggs, larvae, and juvenile stages of Teleostei, Parts I and II, p. 330-375. Fauna and flora of the Bay of Naples, Monograph No. 38. (Translated from Ital., TT68-50346.)

SCHAEFER, M. B., AND C. J. ORANGE.
1956. Studies of the sexual development and spawning of yellowfin tuna (*Neothunnus macropterus*) and skipjack (*Katsuwonus pelamis*) in three areas of the eastern Pacific Ocean, by examination of gonads. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull 1:281-349.

SEKAVEC, G. B., AND G. R. HUNTSMAN.
1972. Reef fishing on the Carolina Continental Shelf. Proc. 15th Annu. Int. Game Fish Res. Conf., p. 76-86.

WALKER, E. T.
1950. Spawning records of fishes seldom reported from North Carolina waters. Copeia 1950:319.

WARNER, R. R.
1975. The adaptive significance of sequential hermaphroditism in animals. Am. Nat. 109:61-82.

MERCURY IN FISH AND SHELLFISH OF THE NORTHEAST PACIFIC. I. PACIFIC HALIBUT, *HIPPOGLOSSUS STENOLEPIS*

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ABSTRACT

A total of 1,227 Pacific halibut, *Hippoglossus stenolepis*, were analyzed for mercury content in the edible muscle tissue. These fish were obtained from five geographical areas within the species range: the Bering Sea, Gulf of Alaska, southeast Alaska, British Columbia, and Washington-Oregon. Mercury was found to be uniformly distributed from nape to tail in the edible muscle tissue. Within each geographical area the mercury concentration increased as the size of the fish increased. The mercury concentration also increased in fish of the same size from the northern to the southern part of the species range.

In the past few years, numerous investigators have examined the distribution and levels of mercury in food, including aquatic food animals, because of the potential health hazards involved. The U.S. Food and Drug Administration established an administrative guideline of 0.50 ppm mercury in fish and shellfish in 1969. Since that time, the guideline has been the subject of several reviews and recently has been proposed as a formal action level (Schmidt 1974).

Since 1970, the Pacific Utilization Research Center (PURC) and the Southeast Utilization Research Center (SEURC) at College Park, Md., have been conducting extensive studies of fish and shellfish taken from marine and inland waters of the United States to determine the extent to which mercury exceeds the guideline in our aquatic resources. This paper reports our findings on mercury in the edible tissue of the Pacific halibut, *Hippoglossus stenolepis* Schmidt.

EXPERIMENTAL PROCEDURE AND METHODS

Halibut were obtained from commercial fishing vessels, fish processing companies, and research vessels of the International Pacific Halibut Commission (IPHC). Data were obtained on area and date of catch, and weight or length of each fish analyzed. Data were also obtained on age and sex when possible.

The five areas of catch were: Washington-Oregon, British Columbia, southeast Alaska, Gulf of Alaska, and the Bering Sea (Figure 1). Commercial halibut are eviscerated at sea, landed as a heads-on eviscerated product, and then beheaded for marketing as fresh or frozen fish. Weights reported here are in pounds for heads-off eviscerated fish because this is the standard practice of the halibut industry. For convenience of some readers who do not normally use our measurement system, approximate metric equivalents in kilograms are given in the tables and figures. When actual weights were impractical to obtain, the lengths of the heads-on fish were used, and heads-off eviscerated weights were estimated using length-weight conversion tables of the IPHC. Age was determined, as described by Hardman and Southward (1965), from otoliths collected at the landing site when circumstances permitted and on all halibut taken by IPHC research vessels.

Before setting up sampling procedures, experiments were carried out to determine the uniformity of distribution of mercury in the muscle of individual fish. No significant differences in concentration of mercury (deviation did not exceed ± 0.03 ppm) were noted in muscle tissue taken from nape, midbody, or tail sections.

Analytical samples consisted of skinned and deboned edible muscle tissue that was normally taken from the nape section just behind the head. Some samples, however, were in the form of steaks and a few consisted of the entire fillets of small fish. Portions, usually about 400 g, taken from the

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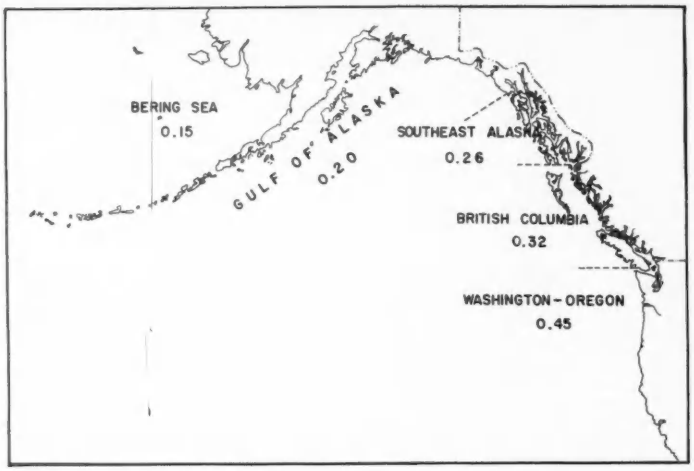

FIGURE 1.—Mean mercury levels in Pacific halibut by area of catch.

nape section were ground in a Hobart grinder[3] equipped with a ⅛-inch (3.2-mm) hole stainless steel plate. Larger steaks and fillets were ground in a Hobart Silent Food Cutter (Model 84181). The comminuted flesh was mixed thoroughly before subsampling for analysis. Because samples were often collected more rapidly than they could be analyzed, they were stored at -29°C until analysis. No change in mercury content was observed in halibut that were analyzed immediately or that had been held in frozen storage in either glass vials or aluminum containers if dehydration was prevented. A halibut sample stored in the above manner and used as an analytical control showed a mean mercury content of 0.88 ± 0.02 ppm over a 2-yr period. This control was analyzed routinely to verify both accuracy and precision of the method.

Total mercury was determined at the PURC by either the method of Munns and Holland (1971) or Malaiyandi and Barrette (1970) as modified by Munns (1972). The former method uses sulfuric, nitric, and perchloric acids for digestion with sodium molybdate as a catalyst, while the Munns' modification utilizes nitric and sulfuric acids for digestion and vanadium pentoxide as a catalyst. Some samples were analyzed at the SEURC by the method of Hatch and Ott (1968) as modified by Uthe et al. (1970). This method uses sulfuric acid for digestion and potassium permanganate as an oxidizing agent.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Final quantitation was by flameless spectroscopy using a Perkin-Elmer Model 403 Atomic Absorption Spectrophotometer at the PURC and by a Varian Techtron Model AA5 at the SEURC. In a collaborative study, the mean deviation between laboratories and methods did not exceed ± 0.02 ppm Hg. All samples were analyzed in duplicate or triplicate, depending upon the method of analysis used. We consider ± 0.05 ppm a significant deviation; therefore, when differences between replicates exceeded this level the samples were reanalyzed. Results are stated in parts per million wet weight.

RESULTS AND DISCUSSION

A total of 1,227 halibut were analyzed for mercury content. Results indicated a relationship between mercury levels and area of catch, age, and size of fish. The results are broken down by the previously described catch areas (Figure 1). The fish taken from each area were separated by weight classes that approximate those used in the halibut industry; the low, high, and mean mercury values for each weight class are given with a frequency distribution of the fish by increasing mercury concentration (Tables 1 through 5). Because we thought that large fish would be more likely to exhibit higher concentrations of mercury, we attempted to obtain as many large fish as was practicable. For this reason our sampling contains a greater percentage of large fish than do the commercial catches from most of the areas dis-

cussed here. Therefore, these data cannot be interpreted to indicate the approximate percentage of the commercial catch that is likely to contain mercury in concentrations over the guideline.

In 152 halibut taken from the Bering Sea, the mercury level in the muscle of 7 fish (5% of the sample) was over the guideline (Table 1). The incidence (percentage over the guideline of the total number of fish within a weight range) was highest among fish weighing more than 80 pounds.

Most of our samples, 761 fish, were taken from the Gulf of Alaska. We found that mercury in the muscle of 38 fish (5% of the sample) exceeded the guideline (Table 2). The highest incidence occurred in fish weighing more than 80 pounds. The weight ranges contributing most to the incidence were those of 126 to 150 pounds and those of more than 150 pounds. These two weight ranges contribute 21% and 32%, respectively, in contrast with only 3% in each of the weight ranges 81 to 100 pounds and 101 to 125 pounds.

The analytical data on 70 fish taken from southeast Alaska area showed that mercury in the muscle of 9 fish (13% of the sample) was 0.50 ppm or higher (Table 3). The small number of fish in the larger weight ranges makes it impossible to be definitive, but it is reasonably clear that in this group, too, the incidence of mercury levels over the guideline was greatest among the largest fish.

Analyses on 163 fish from the British Columbia area showed that 44 of these (27% of the sample) were over the guideline (Table 4). In addition to this relatively high incidence, we saw for the first time the presence of significant numbers of high-mercury-level fish in all weight groups, i.e., 10% of the fish were over the guideline in the 5- to 60-pound range, 75% in the 61- to 80-pound range, 73% in the 81- to 100-pound range, 100% in the 101- to 125-pound range, and 67% in the 126- to 150-pound range. We also saw that the concentration of mercury tended to increase with an increase in the incidence of fish that were over the guideline.

The analytical results on 81 fish taken from the Washington-Oregon area, the most southerly area of the range of the Pacific halibut, showed 29 fish

TABLE 1.—Mercury concentration in heads-off eviscerated Pacific halibut from the Bering Sea.

Weight range Pounds (kg)	No. of fish	Mercury (ppm) in edible muscle tissue										
		Low	High	Mean	<0.25	0.25–0.39	0.40–0.49	0.50–0.59	0.60–0.69	0.70–0.79	0.80–0.89	0.90–0.99	1.00–1.49
					Number of fish								
5-60 (2-27)	88	0.02	0.78	0.11	82	0	2	2	1	1	0	0	0
61-80 (28-36)	33	0.06	0.42	0.15	30	2	1	0	0	0	0	0	0
81-100 (37-45)	16	0.09	0.55	0.19	13	1	1	1	0	0	0	0	0
101-125 (46-57)	10	0.08	1.00	0.32	7	0	1	1	0	0	0	0	1
126-150 (57-68)	5	0.22	0.35	0.27	2	3	0	0	0	0	0	0	0
Total	152	0.02	1.00	0.15	134	6	5	4	1	1	0	0	1

TABLE 2.—Mercury concentration in heads-off eviscerated Pacific halibut from the Gulf of Alaska.

Weight range Pounds (kg)	No. of fish	Mercury (ppm) in edible muscle tissue										
		Low	High	Mean	<0.25	0.25–0.39	0.40–0.49	0.50–0.59	0.60–0.69	0.70–0.79	0.80–0.89	0.90–0.99	1.00–1.49
					Number of fish								
5-60 (2-27)	378	0.01	0.50	0.11	371	4	2	1	0	0	0	0	0
61-80 (28-36)	92	0.05	0.47	0.18	77	13	2	0	0	0	0	0	0
81-100 (37-45)	76	0.05	1.10	0.25	49	15	10	1	0	0	0	0	1
101-125 (46-57)	92	0.03	0.74	0.29	37	36	16	2	0	1	0	0	0
126-150 (57-68)	67	0.12	1.28	0.38	19	23	11	6	3	3	0	1	1
Over 151 (68)	56	0.14	1.05	0.45	8	16	14	6	5	4	2	0	1
Total	761	0.01	1.28	0.20	561	107	55	16	8	8	2	1	3

TABLE 3.—Mercury concentration in heads-off eviscerated Pacific halibut from southeast Alaska.

Weight range Pounds (kg)	No. of fish	Mercury (ppm) in edible muscle tissue										
		Low	High	Mean	<0.25	0.25–0.39	0.40–0.49	0.50–0.59	0.60–0.69	0.70–0.79	0.80–0.89	0.90–0.99	1.00–1.49
					Number of fish								
5-60 (2-27)	33	0.04	0.34	0.12	30	3	0	0	0	0	0	0	0
61-80 (28-36)	10	0.09	1.30	0.33	7	1	1	0	0	0	0	0	1
81-100 (37-45)	9	0.09	0.59	0.28	4	4	0	1	0	0	0	0	0
101-125 (46-57)	13	0.22	0.95	0.46	1	6	1	3	0	0	1	1	0
126-150 (57-68)	3	0.26	0.36	0.31	0	3	0	0	0	0	0	0	0
Over 151 (68)	2	0.50	1.10	0.80	0	0	0	1	0	0	0	0	1
Total	70	0.04	1.30	0.26	42	17	2	5	0	0	1	1	2

TABLE 4.—Mercury concentration in heads-off eviscerated Pacific halibut from British Columbia.

Weight range Pounds (kg)	No. of fish	Mercury (ppm) in edible muscle tissue										
		Low	High	Mean	<0.25	0.25–0.39	0.40–0.49	0.50–0.59	0.60–0.69	0.70–0.79	0.80–0.89	0.90–0.99	1.00–1.49
					Number of fish								
5-60 (2-27)	122	0.04	1.04	0.19	99	7	4	5	3	2	0	1	1
61-80 (28-36)	20	0.12	1.23	0.69	2	2	1	1	4	3	2	3	2
81-100 (37-45)	11	0.10	1.22	0.66	1	2	0	1	2	2	0	0	3
101-125 (46-57)	7	0.50	1.46	0.96	0	0	0	2	0	1	0	1	3
126-150 (57-68)	3	0.25	0.77	0.52	0	1	0	1	0	1	0	0	0
Total	163	0.04	1.46	0.32	102	12	5	10	9	9	2	5	9

TABLE 5.—Mercury concentration in heads-off eviscerated Pacific halibut from Washington-Oregon.

Weight range Pounds. (kg)	No. of fish	Mercury (ppm) in edible muscle tissue										
		Low	High	Mean	<0.25	0.25–0.39	0.40–0.49	0.50–0.59	0.60–0.69	0.70–0.79	0.80–0.89	0.90–0.99	1.00–1.49
					Number of fish								
5-60 (2-27)	75	0.10	1.43	0.42	23	20	9	5	8	3	4	0	3
61-80 (28-36)	6	0.70	1.13	0.88	0	0	0	0	0	2	2	0	2
Total	81	0.10	1.43	0.45	23	20	9	5	8	5	6	0	5

(36% of the sample) were over the guideline (Table 5). None of these fish weighed more than 80 pounds, and only six weighed more than 60 pounds; 31% of the 5- to 60-pound fish and all of the 61- to 80-pound fish were over the guideline. In fish from this area, as in those from British Columbia, the concentrations of mercury increased with the incidence of fish over the guideline.

It is apparent that the mean level of mercury in the edible tissue and the incidence of fish over the guideline increases from the northern to the southern part of the range of the Pacific halibut (Figure 1, Table 6). There is also a relationship between the size of fish and the level of mercury in the muscle. Because of the sex-size relationship of halibut, i.e., males rarely exceed 80 pounds regardless of age, the correlation of mercury to age should be closer than that of mercury to size. However, age data were collected on only 76% of the total sampling, whereas weight was obtained on all samples. For this reason, and as a guide to industry, we have worked mostly with the mercury-size relationship. Evaluation of the data by regression analyses showed that the data are well described by the exponential function ($y = ax^b$). Comparisons of the weights of halibut against

TABLE 6.–Summary of mercury concentration in Pacific halibut.

Area of catch	Number of fish	Mean weight lb	Mean weight kg	Mercury (ppm) Low	Mercury (ppm) High	Mercury (ppm) Mean	Percent of samples exceeding 0.50 ppm
Bering Sea	152	54.6	24.8	0.02	1.00	0.15	4.6
Gulf of Alaska	761	71.8	32.6	0.01	1.28	0.20	5.0
Southeast Alaska	70	67.6	30.7	0.04	1.30	0.26	12.8
British Columbia	163	39.3	17.8	0.04	1.46	0.32	27.0
Washington-Oregon	81	30.3	13.8	0.10	1.43	0.45	35.8

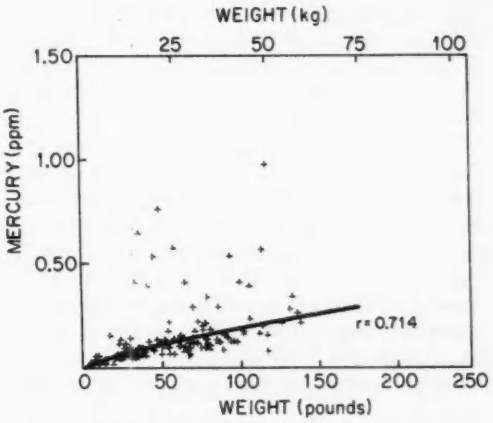

FIGURE 2.–Relationship between heads-off eviscerated weight and mercury concentration in the edible muscle tissue of Pacific halibut from the Bering Sea.

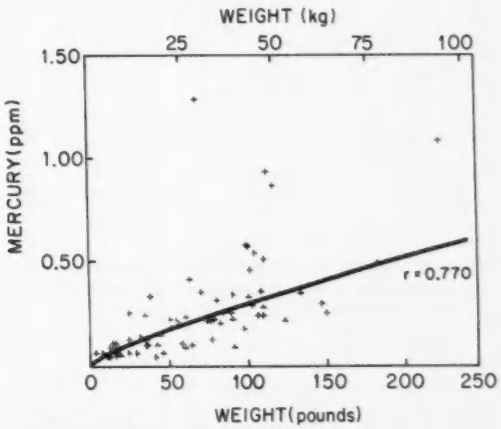

FIGURE 4.–Relationship between heads-off eviscerated weight and mercury concentration in the edible muscle tissue of Pacific halibut from southeast Alaska.

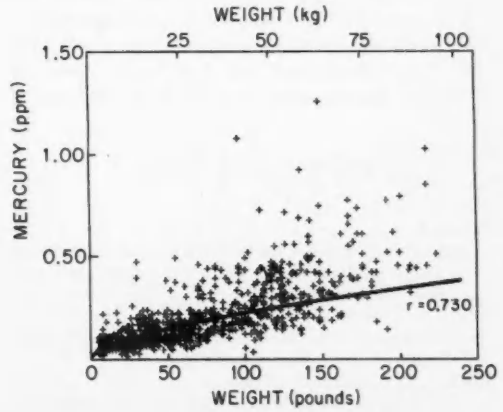

FIGURE 3.–Relationship between heads-off eviscerated weight and mercury concentration in the edible muscle tissue of Pacific halibut from the Gulf of Alaska.

mercury concentrations in the edible tissue for each area are shown in Figures 2 through 6. Correlation coefficients (r values) are shown on each plot and are significant at the 0.1% level. Correlation coefficients between length and mercury were also significant at the 0.1% level within each area and were essentially identical to the correlation coefficients between weight and mercury. This would be expected from the weight-length relationship. Correlation between age and mercury was higher than between weight or length and mercury for fish from the Bering Sea, the Gulf of Alaska, and southeast Alaska; the same for fish from British Columbia; and lower for fish from Washington-Oregon. These correlation coefficients between age and mercury were also significant at the 0.1% level in all areas.

In evaluating the data, areas were used that are either the same as the fishery management areas defined by the International Pacific Halibut Commission (1974) or subdivisions of a management area. This was both logical and practical for the purpose of providing useful information to the halibut industry. The plots of mercury concentration in the edible muscle against weight of fish taken from both the Bering Sea and the Gulf of

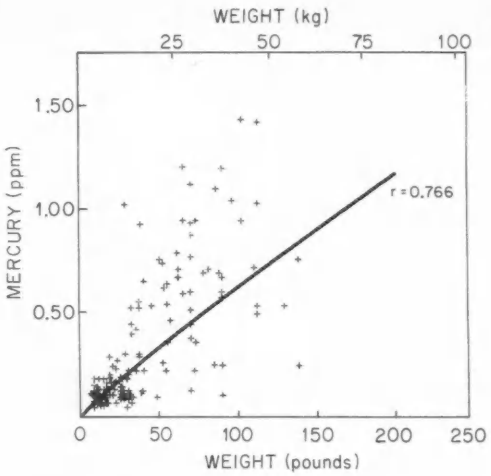

FIGURE 5.—Relationship between heads-off eviscerated weight and mercury concentration in the edible muscle tissue of Pacific halibut from British Columbia.

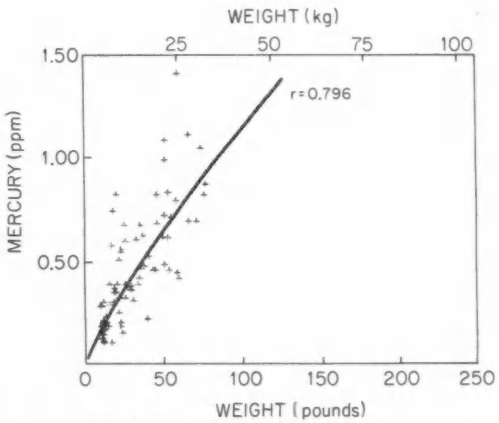

FIGURE 6.—Relationship between heads-off eviscerated weight and mercury concentration in the edible muscle tissue of Pacific halibut from Washington-Oregon.

Alaska (Figures 2, 3) are so similar as to suggest that the environmental and biological factors that determine the rate and extent of deposition of mercury in the muscle are the same in both areas. In any case, the mean level of mercury and the incidence of fish exceeding the guideline increases, while the size of the fish decreases, from north to south.

Increasing concentrations of mercury have been noted in other marine animals as one moves south from the Bering Sea. Anas (1974) pointed out that the harbor seal, *Phoca vitulina richardi*, which is a nonmigratory, inshore carnivore that feeds principally on fish, provides geographical information on local concentrations of contaminants. The livers of harbor seals taken from the Bering Sea contained lower levels of mercury than did those from Washington and Oregon, and those from southern California contained the highest levels. Sablefish, *Anoplopoma fimbria* (Pallas), also shows a similar pattern and will be the subject of another paper in this series.

These observations suggest that the total mercury contamination in the ocean environment (natural plus man-made) increases in a north-to-south direction. Unfortunately, conclusive data to substantiate this hypothesis are not available. Eggerman and Mar (1972), in a review of the research that has been conducted on the various aspects of mercury transport, state that there is a paucity of available data, especially on the biological transport of mercury in marine waters.

ACKNOWLEDGMENTS

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LITERATURE CITED

ANAS, R. E.
1974. Heavy metals in the northern fur seal, *Callorhinus ursinus*, and the harbor seal, *Phoca vitulina richardi*. Fish. Bull., U.S. 72:133-137.

EGGERMAN, T., AND B. MAR.
1972. Mercury in the North Pacific-NORFISH NF01. Cent. Quant. Sci., Univ. Wash., Seattle, 15 p.

HARDMAN, W. H., AND G. M. SOUTHWARD.
1965. Sampling the commercial catch and use of calculated lengths in stock composition studies of Pacific halibut. Int. Pac. Halibut Comm. Rep. 37, 32 p.

HATCH, W. R., AND W. L. OTT.
1968. Determination of sub-microgram quantities of mercury by atomic absorption spectrophotometry. Anal. Chem. 40:2085-2087.

INTERNATIONAL PACIFIC HALIBUT COMMISSION.
1974. Pacific Halibut Fishery Regulations 1974. Int. Pac. Halibut Comm., Seattle, Wash., 5 p.

MALAIYANDI, M., AND J. P. BARRETTE.
1970. Determination of submicro quantities of mercury in biological materials. Anal. Lett. 3:579-584.

MUNNS, R. K.
1972. Mercury in fish by cold vapor AA using sulfuric-nitric acid/V_2O_5 digestion. FDA (Food Drug Admin.) Lab. Inf. Bull. 1500, 8 p.

MUNNS, R. K. AND D. C. HOLLAND.
1971. Determination of mercury in fish by flameless atomic absorption: A collaborative study. J. Assoc. Off. Anal. Chem. 54:202-205.

SCHMIDT, A. M.
1974. Action level for mercury in fish and shellfish. Fed. Regist., 39 (236) Part II: 42738-42740.

UTHE, J. F., F. A. J. ARNSTRONG, AND M. P. STAINTON.
1970. Mercury determination in fish samples by wet digestion and flameless atomic absorption spectrophotometry. J. Fish. Res. Board Can. 27:805-811.

MERCURY IN FISH AND SHELLFISH OF THE NORTHEAST PACIFIC. II. SABLEFISH, *ANOPLOPOMA FIMBRIA*

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ABSTRACT

Sablefish, *Anoplopoma fimbria*, collected from several locations in Alaska, Washington, Oregon, and California were analyzed for their mercury content. Mean mercury level in this species varied with the geographical location of catch, showing a gradual increase in magnitude from north to south; the average size of the specimens decreased in the same pattern, north to south. Of the 692 specimens analyzed in this study, approximately 30% exceeded the U.S. Food and Drug Administration action level of 0.50 ppm mercury. Significant relationships between the size of the fish and mercury content were observed.

Following the Canadian disclosure in March 1970 of high mercury levels in fish caught in Lake St. Clair (Hearnden 1970), the National Marine Fisheries Service (NMFS) initiated studies to determine the distribution and level of mercury in our marine resources. Since that time, the Pacific Utilization Research Center, NMFS, has been conducting extensive screening studies of fish and shellfish of the northeast Pacific in order to evluate the mercury problem as it relates to those species taken by both commercial and sport fisheries. The main objectives were to determine which species contained mercury in excess of the Food and Drug Administration (FDA) action level of 0.50 ppm (Schmidt 1974) and the severity of the problem.

During our preliminary screening of Pacific species, we found that the edible muscle tissue of a number of sablefish contained mercury in excess of the FDA action level. This species ranges from southern California to the Bering Sea (Clemens and Wilby 1961:240). Domestic landings in 1971 were about 6 million pounds (2.7×10^6 kg) (Thompson 1971) but its high value as a smoked product and the availability to the fishermen of additional supplies of this species suggests that landings will increase.

This paper is the second in a series and reports our findings on mercury in the edible muscle tissue of sablefish, *Anoplopoma fimbria* (Pallas). The first paper in the series is on the Pacific halibut, *Hippoglossus stenolepis* Schmidt (Hall et al. 1976).

EXPERIMENTAL PROCEDURE AND METHODS

Most of the sablefish used in this study were obtained by NMFS personnel aboard National Oceanic and Atmospheric Administration (NOAA) research vessels. Some samples were obtained from commercial lots through the cooperation of fish processors in order to cover the range of this species. Samples were obtained from the waters off Alaska, Washington, Oregon, and California. Date and location of catch were recorded for all specimens.

Weights and lengths are reported for heads-off eviscerated fish because this is the standard practice for landing sablefish. Round weights and lengths were converted to the heads-off eviscerated values using conversion tables. Where possible, sex was determined by physical examination when the specimens were eviscerated. Age was determined from the otoliths which were removed at the same time.

Analytical samples consisted of the entire fillets of each fish. The edible muscle tissue was ground in a Hobart grinder[2] equipped with a stainless steel plate perforated with holes ⅛ inch (3.2 mm) in diameter. The comminuted flesh was mixed thoroughly; subsamples were removed, packaged, and stored at -29°C until analysis.

Total mercury was determined by either the FDA method of Munns and Holland (1971) or Malaiyandi and Barrette (1970) as modified by

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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Munns (1972). Final quantitation was by flameless spectroscopy using a Perkin-Elmer Model 403 Atomic Absorption Spectrophotometer.

Results are stated in parts per million wet weight. All samples were analyzed in duplicate and where the deviation for replicates exceeded ±0.05 ppm, the analyses were repeated. Control samples of known value were analyzed routinely to verify both accuracy and precision of the method.

RESULTS AND DISCUSSION

A total of 692 sablefish taken from the Bering Sea and coastal waters of the Pacific Ocean from Kodiak Island, Alaska, to San Diego, Calif., were analyzed for individual mercury content. The specific locations of catch and the mean mercury levels by area are shown in Figure 1. The mean mercury levels show a general increase from north to south, as does the percentage of fish that exceed the FDA action level of 0.50 ppm (Table 1).

TABLE 1.–Summary of mercury concentration in sablefish.

Area of catch	No. of fish	Mean weight Pounds (kg)	Mercury (ppm) Low	High	Mean	% samples over 0.50 ppm
Bering Sea-Kodiak Island	30	2.02 (0.92)	0.02	0.11	0.04	0
Southeast Alaska	120	5.22 (2.37)	0.06	0.77	0.28	5
Washington	121	5.27 (2.39)	0.06	1.28	0.37	23
Oregon	174	4.33 (1.96)	0.06	1.23	0.40	29
Northern California	98	3.14 (1.42)	0.03	0.95	0.26	21
Central California	30	5.68 (2.58)	0.08	0.79	0.47	43
Southern California	119	2.93 (1.33)	0.04	2.11	0.60	72

Effect of the Geographical Location

The fish caught in the Bering Sea and in the vicinity of Kodiak Island were all small (less than 3 pounds [1.4 kg]) and contained very low levels of

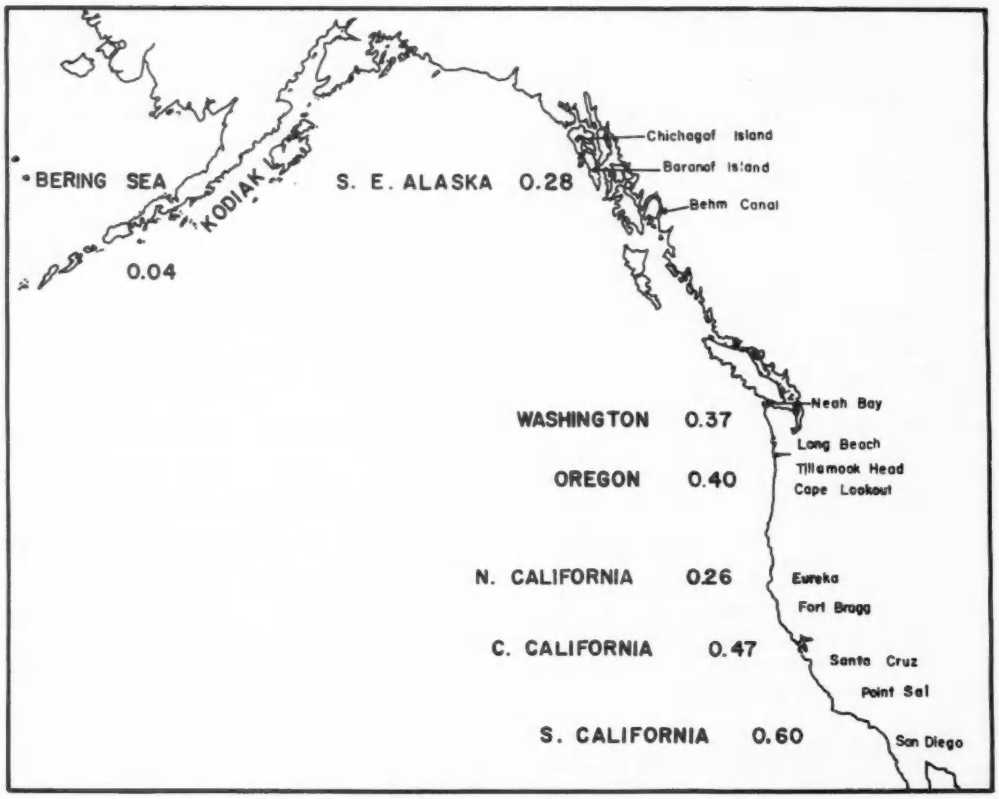

FIGURE 1.–Mean mercury levels (parts per million) in sablefish by area and the specific locations of the catches.

mercury (0.02-0.11, $\bar{x}$ 0.04 ppm). The data for the specimens from these two areas were combined since the samples were relatively few in number, and there was no evidence of any significant differences based on area (Table 1).

A much better weight distribution is seen in the 120 fish from southeast Alaska (Table 2). The fish taken from several locations around Baranof and Chichagof islands (45 specimens) contained a significantly lower mean level of mercury (0.19 ppm) than did the 75 fish taken from the Behm Canal area (0.34 ppm). The only fish (5% of the total sample) from southeast Alaska that exceeded 0.50 ppm mercury were caught off Betton Island, which is in the north arm of Behm Canal. This would indicate a higher level of mercury contamination in the inland waters than in the offshore waters around the outer islands.

Analyses of 121 fish from Washington showed that 23% (28 fish) of the sample exceeded the action level (Table 2). The fish taken from the northern coast off Neah Bay and those taken from the southern coast off Long Beach showed little difference in mercury content.

Of the 174 fish from Oregon, 51 or 29% exceeded the action level (Table 2), which is an increase over that observed in previously discussed areas. A significant part of the total sample (39%) consisted of fish weighing less than 3 pounds (1.4 kg) and of these small fish we observed an increase in the percentage that exceeded 0.50 ppm mercury.

The sampling from northern California (Table 3) consisted of 98 fish of which 62% (61 fish) weighed less than 3 pounds (1.4 kg) and contained low levels of mercury. Only one of these small fish exceeded 0.50 ppm mercury. Of the remaining 37 larger fish, the mercury level of 20 fish exceeded 0.50 ppm. The mean mercury level of the total lot of 98 fish was 0.26 ppm, and 21 fish or 21% exceeded the action level. Considering that this lot represented an atypical weight distribution, it seems likely that both the mean and the percentage of fish exceeding the action level would be higher in a sampling where the number of fish are more uniformly distributed over the weight range.

The 30 fish collected in central California were well distributed over the weight range (Table 3) and 43% of these fish exceeded the action level.

Analytical data on 119 fish from the southern California area showed that 72% (86 fish) exceeded the action level (Table 3). Of this group, 47% weighed less than 3 pounds (1.4 kg). Here, as in Oregon, we saw that smaller fish contained high levels of mercury in comparison to other areas. The weight range of the fish from southern California was small (from 0.5 to 5.5 pounds [0.2-2.5 kg]), but the mercury levels were higher than were observed in any other area.

Effect of Size of Fish

The observations on mercury levels and size of

TABLE 2.—Mercury concentration in heads-off eviscerated sablefish from southeast Alaska, Washington, and Oregon.

Weight range	Southeast Alaska					Washington					Oregon				
	Fish		Mercury (ppm)			Fish		Mercury (ppm)			Fish		Mercury (ppm)		
Pounds (kg)	No.	% over 0.5 ppm	Low	High	Mean	No.	% over 0.5 ppm	Low	High	Mean	No.	% over 0.5 ppm	Low	High	Mean
0.5-2.99 (0.23-1.36)	31	0	0.06	0.23	0.12	23	4	0.07	0.52	0.27	68	7	0.06	0.69	0.25
3.0-3.99 (1.36-1.81)	17	0	0.07	0.48	0.29	21	14	0.12	0.82	0.35	29	24	0.20	0.63	0.43
4.0-4.99 (1.82-2.26)	15	0	0.12	0.40	0.27	22	4	0.06	0.52	0.29	14	43	0.22	0.71	0.48
5.0-5.99 (2.27-2.72)	17	0	0.19	0.46	0.33	14	29	0.26	0.61	0.41	14	21	0.18	0.72	0.45
6.0-6.99 (2.72-3.17)	9	11	0.23	0.61	0.39	11	18	0.12	0.62	0.33	20	55	0.06	1.23	0.51
7.0-7.99 (3.18-3.63)	13	15	0.18	0.56	0.36	14	36	0.08	0.72	0.41	11	64	0.33	0.84	0.55
8.0-8.99 (3.63-4.09)	8	0	0.20	0.47	0.35	3	67	0.48	0.65	0.58	12	58	0.33	0.72	0.52
9.0-9.99 (4.09-4.54)	4	0	0.24	0.48	0.37	7	57	0.15	1.28	0.61	5	80	0.44	1.02	0.68
10.0-10.99 (4.54-4.99)	3	67	0.46	0.77	0.61	3	100	0.52	0.90	0.72	0	—	—	—	—
11.0-11.99 (4.99-5.44)	1	100	0.56	0.56	0.56	3	100	0.50	0.67	0.58	1	100	1.15	1.15	1.15
12.0-12.99 (5.45-5.90)	2	0	0.38	0.48	0.43	—	—	—	—	—	—	—	—	—	—

TABLE 3.—Mercury concentration in heads-off eviscerated sablefish from California.

Weight range	Northern California					Central California					Southern California				
	Fish		Mercury (ppm)			Fish		Mercury (ppm)			Fish		Mercury (ppm)		
Pounds (kg)	No.	% over 0.5 ppm	Low	High	Mean	No.	% over 0.5 ppm	Low	High	Mean	No.	% over 0.5 ppm	Low	High	Mean
0.5-2.99 (0.23-1.36)	61	2	0.03	0.65	0.12	4	0	0.08	0.18	0.13	68	59	0.04	1.74	0.50
3.0-3.99 (1.36-1.81)	8	50	0.20	0.85	0.45	5	40	0.36	0.54	0.46	35	86	0.38	2.11	0.73
4.0-4.99 (1.82-2.26)	14	50	0.22	0.73	0.47	7	29	0.42	0.79	0.53	12	100	0.53	0.88	0.72
5.0-5.99 (2.27-2.72)	9	44	0.22	0.75	0.49	4	25	0.13	0.57	0.40	4	100	0.54	0.83	0.71
6.0-6.99 (2.72-3.17)	2	100	0.70	0.75	0.73	2	0	0.31	0.44	0.37	—	—	—	—	—
7.0-7.99 (3.18-3.63)	2	50	0.32	0.89	0.61	1	100	0.58	0.58	0.58	—	—	—	—	—
8.0-8.99 (3.63-4.09)	1	100	0.95	0.95	0.95	3	100	0.62	0.69	0.66	—	—	—	—	—
9.0-9.99 (4.09-4.54)	1	100	0.53	0.53	0.53	2	100	0.61	0.68	0.64	—	—	—	—	—
12.0-12.99 (5.45-5.90)	—	—	—	—	—	1	100	0.71	0.71	0.71	—	—	—	—	—
13.0-13.99 (5.90-6.35)	—	—	—	—	—	1	100	0.61	0.61	0.61	—	—	—	—	—

sablefish are analogous to what was found in Pacific halibut (Hall et al. 1976); i.e., mercury levels increased from north to south until at the southern part of the range even small fish exhibited high mercury levels. Anas (1974) observed a similar pattern in the harbor seal, *Phoca vitulina richardi*.

There appears to be a direct relationship between the size of the sablefish and the mercury level found in the muscle. Comparisons between weight and mercury level for fish from each area are given in Figures 2-8. The exponential function, $y = ax^b$, was used for the statistical evaluation of the data. Length-to-mercury relationships are very similar to those for weight-to-mercury and are not shown for this reason. Correlation coefficients (r values) are shown on each plot, and the relationship between weight and mercury was highly significant (0.1% level) in all areas except in the Bering Sea-Kodiak Island area where the relationship was not significant.

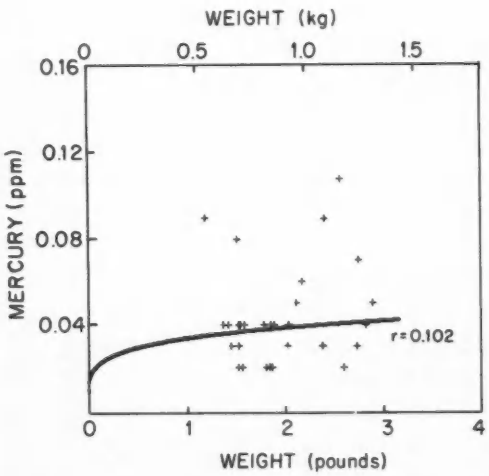

FIGURE 2.—Relationship between heads-off eviscerated weight and mercury concentration in muscle tissue of sablefish from the Bering Sea-Kodiak Island, Alaska.

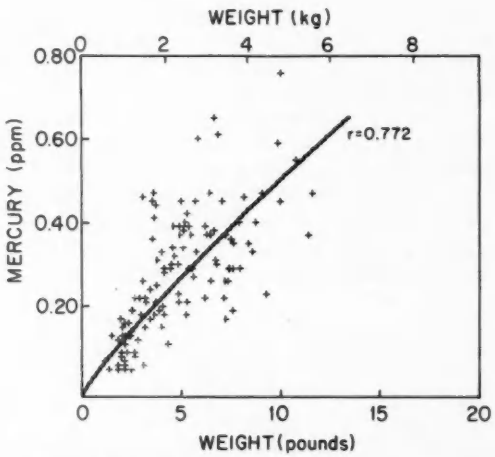

FIGURE 3.—Relationship between heads-off eviscerated weight and mercury concentration in muscle tissue of sablefish from southeast Alaska.

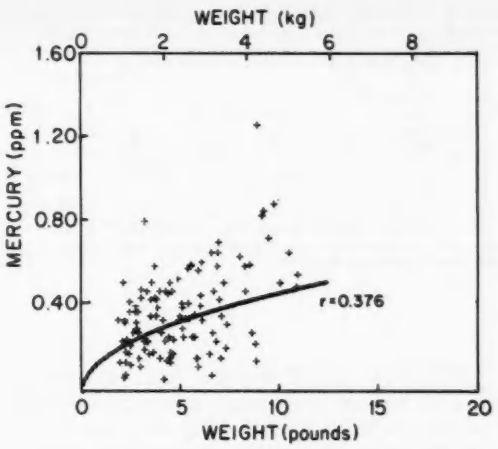

FIGURE 4.—Relationship between heads-off eviscerated weight and mercury concentration in muscle tissue of sablefish from Washington.

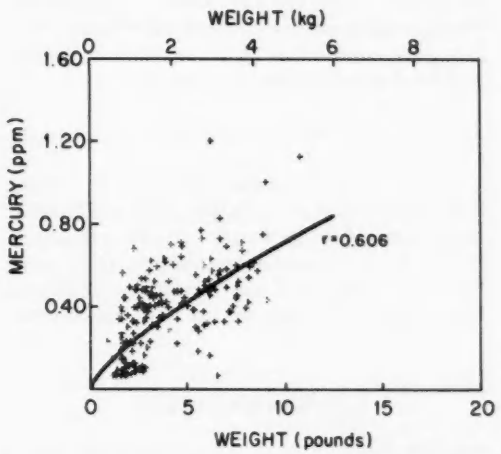

FIGURE 5.—Relationship between heads-off eviscerated weight and mercury concentration in muscle tissue of sablefish from Oregon.

Effect of Age

Since the female sablefish grows faster and attains a larger size than the male (Clemens and Wilby 1961), it would seem logical to assume that the correlation between age and mercury level might be better than that of weight and mercury level. However, higher correlation coefficients exist between weight and mercury than between age and mercury in all areas except Oregon.

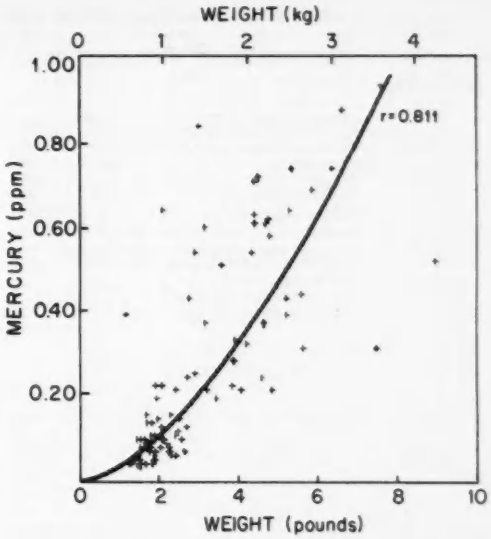

FIGURE 6.—Relationship between heads-off eviscerated weight and mercury concentration in muscle tissue of sablefish from northern California.

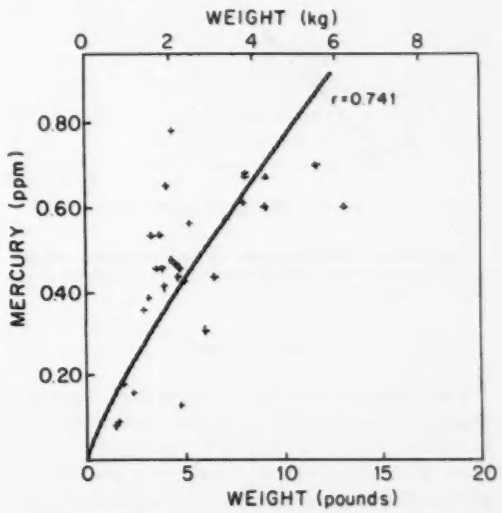

FIGURE 7.—Relationship between heads-off eviscerated weight and mercury concentration in muscle tissue of sablefish from central California.

Relationships between age and mercury are significant in all areas except Washington (Table 4). Age was not obtained on fish from the Bering Sea-Kodiak Island area.

TABLE 4.—Correlation coefficients for relationship of mercury level in the edible flesh to weight, age, and sex of sablefish.[1]

Area of catch	Number of fish	Weight to mercury	Number of fish	Age to mercury	Number of females	Weight to mercury	Number of males	Weight to mercury
Bering Sea-Kodiak Island	30	[2]0.102	—	—	—	—	—	—
Southeast Alaska	120	0.772	103	0.684	71	0.868	43	0.762
Washington	121	0.376	38	[2]0.179	30	0.731	10	[2]0.349
Oregon	174	0.606	80	0.693	116	0.657	53	0.480
Northern California	98	0.811	63	0.558	—	—	—	—
Central California	30	0.741	28	[3]0.430	17	[4]0.630	12	[4]0.758
Southern California	119	0.748	97	0.439	30	0.661	11	[2]0.203

[1]Correlation coefficients significant at the 0.1% level unless otherwise indicated.
[2]Not significant.
[3]Significant at 5% level.
[4]Significant at 1% level.

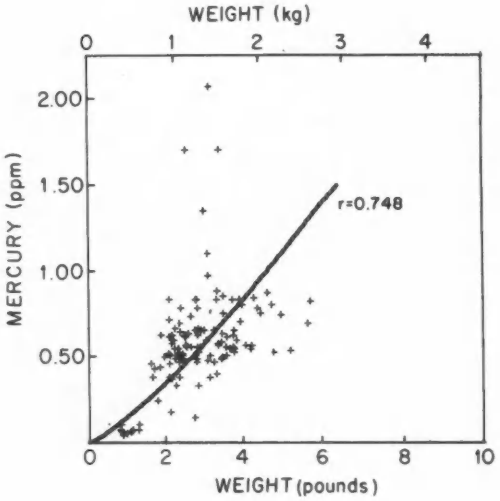

FIGURE 8.—Relationship between heads-off eviscerated weight and mercury concentration in muscle tissue of sablefish from southern California.

Effect of Sex

The females show better correlation between weight and mercury than do the males, and correlation coefficients are significant for females from all areas (Table 4). Correlation coefficients for weight to mercury are also significant for males in all areas except Washington and southern California. Sex was not obtained on fish from the Bering Sea-Kodiak Island or northern California.

Effect on Utilization of Sablefish

It is apparent that sablefish can accumulate mercury in amounts that exceed the maximum level permitted in fish by the FDA. Spinelli et al. (1973) noted that fish withheld from food use due to high mercury levels constitute a significant loss to the industry and showed that such losses could be reduced by using a cysteine treatment to lower the mercury content of the fish during processing. Teeny et al. (1974) conducted a similar study on the reduction of mercury in sablefish, and found that up to 80% of the mercury present in the edible tissue could be removed. Processing techniques of this type could result in all sablefish being acceptable for human consumption.

ACKNOWLEDGMENTS

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LITERATURE CITED

ANAS, R. E.
1974. Heavy metals in the northern fur seal, *Callorhinus ursinus* and harbor seal, *Phoca vitulina richardi*. Fish. Bull., U.S., 72:133-137.

CLEMENS, W. A., AND G. V. WILBY.
1961. Fishes of the Pacific Coast of Canada. 2d ed. Fish. Res. Board Can., Bull. 68, 443 p.

HALL, A. S., F. M. TEENY, L. G. LEWIS, W. H. HARDMAN, AND E. J. GAUGLITZ, JR.
1976. Mercury in fish and shellfish of the northeast Pacific. I. Pacific halibut, *Hippoglossus stenolepis*. Fish. Bull., U.S. 74:783-789.

HEARNDEN, E. H.
1970. Mercury pollution Fisheries Department acts quickly to safeguard public health. Fish. Can. 22(10):3-6.

MALAIYANDI, M., AND J. P. BARRETTE.
1970. Determination of submicro quantities of mercury in biological materials. Anal. Lett. 3:579-584.

MUNNS, R. K.
1972. Mercury in fish by cold vapor AA using sulfuric-nitric acid/V_2O_5 digestion. FDA (Food Drug Admin.) Lab. Inf. Bull. 1500, 8 p.

MUNNS, R. K., AND D. C. HOLLAND.
1971. Determination of mercury in fish by flameless atomic absorption: A collaborative study. J. Assoc. Off. Anal. Chem. 54:202-205.

SCHMIDT, A. M.
1974. Action level for mercury in fish and shellfish. Fed. Regist. 39(236) Part II:42738-42740.

SPINELLI, J., M. A. STEINBERG, R. MILLER, A. HALL, AND L. LEHMAN.
1973. Reduction of mercury with cystein in comminuted halibut and hake fish protein concentrate. J. Agric. Food Chem. 21:264-268.

TEENY, F. M., A. S. HALL, AND E. J. GAUGLITZ, JR.
1974. Reduction of mercury in sablefish (*Anoplopoma fimbria*) and the use of the treated flesh in smoked products. Mar. Fish. Rev. 36(5):15-19.

THOMPSON, B. G.
1971. Fishery Statistics of the United States. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Stat. Dig. 65, 424 p.

ECOLOGY OF HAWAIIAN SERGESTID SHRIMPS (PENAEIDEA: SERGESTIDAE)

JOHN F. WALTERS[1]

ABSTRACT

This paper describes the vertical distribution and migration, population size, seasonal size-frequency distribution, and diet of 20 species of sergestid shrimps collected between 1970 and 1973 in the vicinity of Oahu, Hawaii.

During the daytime, half-red sergestids live between 450 and 725 m, while all-red sergestids range from 650 to at least 1,200 m. At night all but two species migrate into the 0- to 300-m region, half-red and all-red groups mixing together. One nighttime group lives above 100 m, another lives between 125 and 300 m. Moonlight depresses the shallow group below 150 m; it has little effect on the deep group. In addition, some species stop migrating around full moon, remaining at their daytime depths.

All species examined eat zooplanktonic crustacea in the 1- to 3-mm size range. Some species can also utilize smaller zooplankton around 0.4-0.6 mm. This ability is unrelated to the enlarged maxillipeds found in some species.

Most species appear to spawn mostly during the spring, although ovigerous females can be found at any time of the year. Life span appears to be 1 yr for all species except *Sergia bisulcata*, which lives 2 yr. One species does not reproduce in Hawaiian waters.

Hawaiian sergestids are specialized by size, morphology, and vertical distribution. The most closely related species pairs are always separated by size. The Hawaiian sergestid assemblage is very similar to assemblages reported from two areas of the tropical Atlantic.

Shrimps of the family Sergestidae (Decapoda, Penaeidea) are one of the most characteristic groups of micronekton over much of the open ocean. They dominate the crustacean micronekton over large areas of the North Pacific, where they form sound-scattering layers (Barham 1957) and feed baleen whales (Omori et al. 1972). Two speciose sergestid assemblages have been described from the subtropical Atlantic by Foxton (1970) and Donaldson (1973, 1975). This paper examines the sergestid assemblage from the central Pacific near the Hawaiian Islands, reporting vertical distribution and migration, abundance, growth and reproduction, and diet.

MATERIALS AND METHODS

Sampling Area

All the sergestids examined in this study were collected off the leeward (west) coast of Oahu, Hawaii at about lat. 21°30′N, long. 158°20′W. Most trawling was done 10-25 km offshore in water 1,500-4,000 m deep. Physical and chemical data for this area, as well as the nearby Gollum Station (lat. 22°10′N, long. 158°00′W), have been reported by Gundersen et al. (1972) and Gordon (1970). The mixed layer is 50-80 m thick with a temperature of 23°-26°C. The annual variation in temperature of the mixed layer is only about 3°C (Gordon 1970). A broad thermocline extends to approximately 500 m, where the temperature is 5°-7°C. Salinity varies from 34.0 ‰ at 400-500 m to 35.2 ‰ at 100 m; oxygen varies from 7 mg/liter at 100 m to 1 mg/liter at 700-900 m. The water is very clear. In situ measurements of irradiance to 500 m at lat. 28°29′N, long. 155°14′W in August 1972 gave an extinction coefficient of 0.029 m^{-1} at a wavelength of 471 nm for depths below 200 m; surface irradiance at 471 nm was 7×10^2 $\mu W/cm^2$ per nm, decreasing to 1×10^{-4} $\mu W/cm^2$ per nm at 500 m (E. M. Kampa, pers. commun.). Annual net primary productivity has been estimated at 50 g C/m^2 (S. A. Cattell in T. A. Clarke 1973:431). Nakamura (1967) found an annual mean standing crop of zooplankton of 2.6 g/m^2 in the upper 200 m.

The sampling area was chosen as the deep water nearest to Honolulu. It has the further advantage of being in the lee of Oahu under normal tradewind conditions, an important practical consideration when working from RV *Teritu*. In

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spite of its proximity to land, the area appears to be representative of the open waters of the central North Pacific. Meroplankton is sometimes abundant, particularly larval stomatopods, but never dominates the zooplankton. The light regime at night may be affected by light from the urbanized areas of Oahu, although direct light from Honolulu is shielded by mountains. Doty and Oguri (1956) found enhanced values of primary productivity near the Hawaiian Islands (the "island mass effect"), but Gilmartin and Revelante (1974) found this effect only within about 1 km of land. The advantages of nearness to port and convenience of study greatly outweigh the potential disadvantages of being affected by nearshore processes.

Vertical Distribution: Teuthis Sampling Program

Most of the material studied was collected during the "Teuthis" program, a series of 23 cruises during 1971-73 by the University of Hawaii's RV *Teritu*. The primary objective of the program was to determine the vertical distributions of the various species of micronekton during the daytime and at night. For this purpose an extensive series of horizontal tows was made using a modified Tucker trawl (MT) with a mouth 3 m wide. The trawl can be opened and closed at the desired sampling depth, avoiding contamination of the sample by organisms from shallower depths during setting and retrieval. It is lined with knotless nylon mesh, with apertures about 7 mm in diameter. The cod end is a 1-m plankton net of 303-μm Nitex.[2] Mounted on the trawl is a time-depth recorder (Benthos 1170) which provides a record of the depths sampled by the trawl.

This basic configuration was extensively modified during the course of the sampling program to obtain more reliable operation and better data. The original acoustic-controlled opening-closing system (Inter-Ocean) was replaced by a more reliable messenger-operated double-trip mechanism (modified General Oceanics No. 4020). A digital flowmeter (General Oceanics No. 2030) was added at the beginning of 1972, giving a more accurate estimate of the volume of water sampled by the trawl. An acoustic telemeter (AMF No. 1024) allowed real-time monitoring of trawl depth beginning in November 1972; earlier tows wandered vertically over 10-20% of their maximum depth.

The limitations of time and unreliability of sampling gear forced abandonment of plans for a uniform series of standard tows. Each cruise attempted instead to sample depths not yet sampled or to answer questions raised by previous sampling. Informal as this protocol was, the actual depths sampled often differed greatly from the plan. Before a telemeter was available, the sampling depth was set by the amount of wire paid out; two tows with the same amount of wire out often showed a twofold variation in modal depth. Over the course of the program the upper 1,200 m was sampled rather thoroughly, with a few deeper tows down to 2,300 m.

A typical cruise lasted 4 days. On each day two tows were made during the daytime and two at night, avoiding the twilight periods when many mid-water animals are migrating. Tows sampled for 3 h at a towing speed of about 4 knots. The catch was immediately placed in chilled seawater, and live specimens were removed to an aquarium for observation. The rest of the catch was sorted and preserved in buffered 5% Formalin seawater. The inside of the net was picked clean of animals after each tow to prevent contamination of subsequent tows. Physical conditions recorded included ship's position at the beginning and end of sampling, weather conditions and sea state, time of sunrise and sunset, and lunar phase. Bathythermograph casts were made during the early cruises, later replaced with expendable bathythermograph casts; at least one was taken per cruise (Maynard et al. 1975). The 1973 cruises also recorded biological sound scattering at 25 kHz and surface light irradiance (Walters in prep.). In the laboratory, the sergestids were sorted to species, sexed, and counted, and the carapace length (CL) from the base of the rostrum to the posterior margin of the carapace at the dorsal midline was measured to the nearest 0.1 mm with an eyepiece micrometer in a dissecting microscope.

Between February 1971 and June 1973, 16 cruises produced 160 horizontal tows (Table 1). Daytime (DAY) tows were lumped together, but nighttime tows were divided into tows during the dark of the moon or with the moon obscured by clouds (NIGHT) and tows made under substantial amounts of moonlight (MOON). Total trawling time for each 25-m interval of the water column to 1,500 m for the entire series was calculated from time-depth records (Table 2).

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.–Summary of sampling, 1970-73.

Cruise	Dates	Samples	Remarks
70-12	8-10, 13-17 Dec. 1970	31	3-m IKMT[1] horizontal open tows
Teuthis IV	19-21 Feb. 1971	8	3-m MT[2] horizontal opening-closing tows
Teuthis V	15-19 Mar. 1971	14	
Teuthis VI	22-26 Apr. 1971	12	
Teuthis VII	24-26 May 1971	7	
Teuthis VIII	21-25 June 1971	12	
Teuthis IX	30 July-1 Aug. 1971	8	
Teuthis X	22-24 Sept. 1971	1	
Teuthis XI	28 Jan.-1 Feb. 1972	8	
Teuthis XII	25-29 Feb. 1972	6	
Teuthis XIII	25-29 Mar. 1972	11	
Teuthis XV	23-27 May 1972	11	
Teuthis XVI	29 June-2 July 1972	12	
Teuthis XVII	1-5 Aug. 1972	10	
Teuthis XIX	3-7 Nov. 1972	12	
Teuthis XXI	4-7 May 1973	13	
Teuthis XXIII	13-17 June 1973	15	
Teuthis XVIII	30 Sept.-4 Oct. 1972	25	3-m IKMT shallow and deep oblique open tows
Teuthis XXII	23-27 May 1972	15	
DSB III	2-3 Feb. 1973	14	3-m MT horizontal and oblique open tows
Echo IV	5-11 Dec. 1973	25	3-m IKMT stratified oblique open tows

[1]IKMT = Isaacs-Kidd midwater trawl.
[2]MT = modified Tucker trawl.

Oblique Series: Teuthis XVIII and XXII

Teuthis XVIII, 30 September to 4 October 1972, represented a departure from our normal sampling program. It consisted of a series of oblique tows with a 3-m Isaacs-Kidd midwater trawl (IKMT) designed to assess the relative importance in numbers and biomass of the various groups of micronekton, and also to determine the proportion of the mid-water community undergoing diurnal vertical migration (Table 1). Two series of oblique tows were taken: "deep" tows from the surface to 1,200 m, and "shallow" tows from the surface to 400 m. The catches were preserved unsorted in 5% Formalin seawater and returned to the laboratory, where they were sorted into the major taxa, blotted dry, counted, and weighed. Further details of sampling methods and results can be found in Maynard et al. (1975). The sergestids were divided into half-red and all-red types, counted, and weighed. They were later separated by species, counted, and sexed, and the carapace length measured.

Teuthis XXII, 23-27 May 1973, followed the same sampling protocol as Teuthis XVIII, with series of shallow and deep oblique tows. Sergestids from this cruise were separated by species, counted, and sexed, and the carapace length measured.

Effects of Moon: 70-12 and Echo IV

The Teuthis cruises were unevenly spaced in time, making it difficult to use the data for studying growth rates and other aspects of population dynamics. In particular there were no cruises at all between early November and late January. To fill this gap in the seasonal coverage, I examined the sergestids from the December 1970 cruise of T. A. Clarke (70-12). This cruise used a 3-m IKMT for an extensive series of 2- and 3-h horizontal open tows in the upper 1,250 m of the water column (Table 1). Further details of sampling can be found in T. A. Clárke (1973). While the material from this cruise helped balance the seasonal data, it raised new questions about the vertical distribution of sergestids. Many of the species in the 70-12 samples showed abnormal vertical distributions. Since the cruise took place near full moon, it appeared that the abnormalities, in particular the absence of normal vertical migration patterns in some species until the final two nights of the cruise, were related to lunar phase. Unfortunately, shallow and deep tows were not taken on the same night, so it was unclear whether entire populations were affected and on which night normal behavior resumed.

The sampling program of Echo IV attempted to clarify these problems. We planned to make shallow and deep oblique tows with a 3-m IKMT from first quarter to full moon in an attempt to find when vertical migration ceased. Mechanical difficulties postponed the cruise until three nights before full moon; migration had already ceased by this time. The sampling protocol called for a shallow tow, either 0-200 m or 200-400 m; an

TABLE 2.–Number of tows and total towing time for each depth interval, 0-1,500 m, Teuthis sampling program.

Depth (m)	DAY			NIGHT			MOON		
	No. of tows	No. of tows >10 min	Total min	No. of tows	No. of tows >10 min	Total min	No. of tows	No. of tows >10 min	Total min
	3	0	6	7	3	433	13	0	38
	3	0	6	7	4	425	14	4	514
	3	0	8	7	5	313	13	5	350
	3	0	9	8	5	385	12	5	604
100 –				–			–		
	3	1	124	6	6	381	8	2	124
	4	2	95	6	3	336	8	2	51
	3	1	91	6	6	486	8	5	530
	3	1	106	5	5	306	6	4	324
200 –				–			–		
	4	2	121	1	0	2	5	4	204
	4	2	83	2	1	131	3	2	335
	3	2	105	4	4	337	2	1	180
	2	2	116	5	3	149	3	3	208
300 –				–			–		
	3	3	122	3	2	118	4	3	199
	4	4	115	3	3	61	2	2	162
	4	4	150	3	3	48	1	0	9
	4	3	302	4	4	123	0	0	—
400 –				–			–		
	6	4	160	5	5	266	2	1	42
	8	6	291	4	2	135	2	2	211
	13	9	609	3	3	241	2	2	95
	14	11	406	5	2	94	2	2	49
500 –				–			–		
	10	7	508	3	2	86	2	2	236
	9	8	260	4	2	140	1	1	14
	12	9	370	4	1	23	1	0	5
	14	11	492	4	1	75	2	0	11
600 –				–			–		
	15	14	559	6	4	216	3	2	71
	10	7	225	6	4	147	4	4	293
	8	5	274	7	3	82	6	5	205
	12	7	371	5	3	172	5	4	210
700 –				–			–		
	13	8	388	4	3	249	5	5	115
	14	10	459	3	1	40	3	3	143
	12	9	341	3	2	88	2	1	35
	13	11	449	2	1	51	2	2	114
800 –				–			–		
	11	7	379	4	2	91	3	2	74
	9	7	206	4	2	119	3	2	62
	7	6	190	4	1	29	3	2	69
	9	6	165	3	2	62	2	1	13
900 –				–			–		
	10	6	185	3	1	57	2	1	24
	10	7	179	2	1	44	1	0	2
	9	4	197	2	2	29	1	0	4
	8	4	148	1	1	17	1	0	5
1,000 –				–			–		
	5	3	166	1	0	6	1	0	4
	5	2	209	1	0	7	1	0	4
	5	2	62	1	0	7	1	0	8
	4	1	26	1	1	15	1	1	12
1,100 –				–			–		
	3	2	47	1	1	85	1	0	8
	3	2	126	1	0	2	1	1	48
	2	1	14	0	0	—	1	1	12
	2	2	42	0	0	—	0	0	—
1,200 –				–			–		
	2	2	89	0	0	—	0	0	—
	3	2	39	0	0	—	0	0	—
	3	1	62	0	0	—	0	0	—
	3	2	71	0	0	—	0	0	—
1,300 –				–			–		
	3	3	53	1	1	10	0	0	—
	3	3	104	1	1	20	0	0	—
	3	2	59	1	1	45	0	0	—
	2	1	16	1	1	23	0	0	—
1,400 –				–			–		
	2	1	18	1	0	7	0	0	—
	2	2	27	2	2	80	0	0	—
	1	0	6	2	0	10	0	0	—
	1	1	16	2	0	8	0	0	—
1,500 –				–			–		

intermediate tow of 400-600 m; and a deep tow of 400-1,200 m, each night of the cruise. Daytime trawling investigated possible moon-related changes in the daytime distribution of sergestids and included a 400- to 800-m tow and a 600- to 1,000-m tow each day. The actual depths sampled by the trawl deviated somewhat from the protocol, as we used no telemetry on the trawl. The last daytime tow was an all-day affair sampling from 1,100 to 1,900 m. The sergestids from this cruise were identified to species and counted, but not sexed or measured.

Feeding Study: DSB III

An important problem in any study of feeding in mid-water animals is the effect of the sampling gear on feeding behavior. A mid-water trawl concentrates animals in the cod end to unnaturally high densities. Often the trawl lumps together animals from different depth zones. A predator feeding on the contents of the cod end is likely to eat prey it would not normally take in the natural state, either because predator and prey do not occur at the same depth or because the prey can normally escape the predator. Examination of sergestid stomach contents from the Teuthis series suggested that many shrimp had been feeding in the trawl. A modification of the trawl became necessary to get reliable feeding data.

The DSB III cruise of 2-3 February 1973 was designed to investigate the feeding behavior of mid-water animals. The MT was modified by tieing off the cod end ahead of the plankton net, allowing zooplankton to escape through the meshes. The trawl mouth was tied open. Daytime and nighttime oblique and horizontal tows were taken, the main objective being to obtain as large and varied a collection of mid-water animals as possible without much concern for their depth of capture (Table 1). The samples were preserved in 5% Formalin seawater and returned to the laboratory, where the sergestids were sorted out and their stomach contents identified.

Using the MT in this fashion produced one unexpected bonus. In addition to flushing out prey-sized zooplankton, the water current forced the catch and the inner lining of the net through the coarse outer net in pockets. Within each pocket the animals were firmly held by the force of the water, preventing movement and feeding. Future feeding studies might profit from deliberately designing this effect into the sampling gear.

Analysis of Vertical Distribution Data: The Contamination Problem

Most previous studies of vertical distribution (e.g., Foxton 1970, T. A. Clarke 1973, Donaldson 1975) have assumed that all the animals captured in a horizontal tow were taken at a single depth. While such an assumption simplifies the presentation and interpretation of the data, it can produce a misleading picture of the vertical structure of the mid-water community if the tows actually fish over a substantial depth range. Open trawls like the IKMT are the most susceptible to contamination of the catch by animals from other depths, since they fish during setting and retrieval. In this case, contamination usually takes the form of shallow-living animals appearing to have been captured below their normal depth. Rapid setting and retrieval can minimize but not eliminate the problem (T.A. Clarke 1973). Foxton (1970) and Donaldson (1975) have shown that animals from other depths can contaminate IKMT samples even when the trawl is fitted with opening-closing cod end buckets. Some animals become temporarily entangled in the net early in the tow. When they break free later on, the trawl may be fishing at a different depth, resulting in a sample that mixes shallow and deep animals in an unknown proportion.

Even an opening-closing trawl like the MT can give misleading results if it is allowed to wander vertically while open. In such a case, assigning the entire catch to the modal depth broadens out the apparent vertical range in both directions. Our experience has shown that towing the MT deeper than 200 m results in substantial vertical wandering unless its depth is constantly monitored and adjusted. Since a working telemeter was available only during the latter part of our program, most of our "horizontal" tows actually have a vertical range of 50-100 m. The problem increases with depth; tows below 800 m commonly wander 200 m or more. Assigning the catch to a modal depth would produce a misleading vertical distribution pattern.

The vertical distribution diagrams presented in this paper allow for vertical wandering of the trawl and for unequal sampling time with depth. Only horizontal tows are considered. The water column is divided into 25-m zones, and the amount of time each tow spent in each zone is determined from the various depth zones in proportion to the time towed in each zone. Let c_i be the number of

shrimp captured by the ith tow and $t_{i,j}$ be the amount of time tow i spent in the jth depth zone. Then the proportional catch $c_{i,j}$ from the ith tow in the jth depth zone is

$$c_{i,j} = \frac{c_i}{t_{i,j}}. \quad (1)$$

For each depth zone j, summing proportional catches from all tows and dividing by total trawling time in the zone gives the catch rate r_j:

$$r_j = \frac{\sum_i c_{i,j}}{\sum_i t_{i,j}}. \quad (2)$$

Ideally, the catch rate is proportional to the population density, so that dividing the catch rate by trawl filtering rate gives an estimated population density; i.e.,

$$D_j = \frac{r_j}{M_e \cdot f \cdot v}, \quad (3)$$

where D_j is the estimated population density in the jth zone, M_e is the effective mouth area of the trawl (because of the design of the trawl, this quantity decreases with increasing towing speed), f is the filtering efficiency of the trawl, and v is the towing speed.

Proportional allotment of the catch by this method assumes that a particular shrimp is equally likely to have been captured at any instant during the tow. This assumption is clearly false for tows that spend only part of their time in the shrimp's actual depth range. However, spurious catch rates outside the actual depth range are minimized by additional tows in these zones that do not enter the actual depth range and do not catch shrimp; these tows increase the denominator of Equation (2) without increasing the numerator. It follows that this method of estimating vertical distributions works best when each depth zone is sampled many times.

Table 2 shows that during the daytime all depth zones between 400 and 1,075 m were sampled at least five times and that at least five tows spent more than 10 min in all zones between 425 and 950 m. Nighttime sampling was less thorough because tows were split into two groups on the basis of moonlight. In both groups all zones in the upper 200 m were sampled at least five times, as was the 600- to 700-m range (NIGHT) and 650- to 725-m range (MOON). NIGHT tows in the 200- to 225-m zone sampled only 2 min; estimated population densities for this zone, while generally plausible-looking, should be regarded cautiously. The 0- to 25-m zone for MOON tows were sampled many times for brief periods by open tows that spent nearly all their time at depths of 50-150 m, but was never sampled extensively by any tow. Many species show spuriously high estimated population densities in this zone. There were no NIGHT tows between 1,150 and 1,300 m, and no MOON tows between 375 and 400 m or below 1,175 m. Nighttime sampling was generally sparse below 800 m, and the estimated population densities for this region are very crude.

A second major assumption of this method of presenting vertical distribution data is that the vertical distribution remains constant throughout the sampling period, allowing data from many different cruises to be summed together. The resulting estimated population densities represent an average over the entire sampling period. The actual vertical structure on any given cruise may vary considerably from this average. The separation of nighttime tows into NIGHT and MOON tows is the only systematic attempt to show variations in vertical distribution; other variations are discussed in the species accounts.

Presentation of Results

A brief explanation will aid in interpreting the vertical distribution figures that follow (e.g., Figure 1). Catch rates were converted to estimated population densities in numbers per 10^5 m^3 by assuming an average trawling speed of 2 m/s, effective trawl mouth area of 5.1 m^2 (at 2 m/s), and filtering efficiency of 90%. DAY, NIGHT, and MOON (see above) distributions are shown for the entire population as histograms on the right side of the figure. The number to the right of each histogram is the sample size. In addition, the catches were divided into size classes, and population densities were estimated by the same method for each size class. Species with a maximum carapace length less than 17.0 mm were divided into 0.5-mm classes, while larger species were divided into 1.0-mm classes. The result was an array of estimated population densities as a function of size and depth. Interpolation produced a series of contours of equal population density. The lowest contour level represents 0.2 shrimp per 10^5 m^3 per mm CL; each successive contour level

represents a tenfold increase over the previous one.

The oblique tows of September 1972 (Teuthis XVIII) and May 1973 (Teuthis XXII) provided data that yield two estimates of the population densities of the various species, using the method of Maynard et al. (1975). Summing over the entire water column the depth-specific population densities obtained from the horizontal tows provides a third estimate of population densities. The results of these estimates are reported as numbers per 100 m^2 of ocean surface in Table 3. Sample sizes and standard deviations are given for the mean values of the oblique series. Because of the nature of the calculations for the horizontal tows, no standard deviations can be figured, but the variation is probably of the same order as those of the oblique series, since horizontal tows sampled each depth interval about the same number of times and for roughly the same total amount of time as the oblique tows.

The Teuthis data are poorly suited for investigating growth and reproduction of sergestids. The sampling program was designed primarily to investigate the vertical distribution of mid-water animals. Depth coverage varied widely from cruise to cruise, and the cruises were spaced irregularly throughout the year. In order to smooth the irregularities as much as possible, the data are lumped into 3-mo periods. The cruises invoved are:

Jan. - Mar.	T4, T5, T11, T12, T13
Apr. - June	T6, T7, T8, T15, T16, T21, T23
July - Sept.	T9, T10, T17, T18
Oct. - Dec.	T19, 70-12.

Histograms show the size-frequency distribution of males and females for each species. For *Sergestes pectinatus* only, data from the oblique series of May 1973 (Teuthis XXII) are added into the second quarter histogram.

Because of the problem of feeding in the trawl (discussed above), only the stomach content data from DSB III (February 1973) are presented. Table 4 shows the average condition of the stomach contents for each tow. The two indices reported represent the quantity of food present and its state of digestion. Both are based on an arbitrary scale of 1 to 5:

Contents	*Digestion*
1. Packed full, distended.	Whole animal, with little evidence of digestion.
2. More than half full.	Body still mostly intact, appendages separated, some digestion of soft parts.
3. 25-50% full.	All soft parts digested, cuticle remaining, usually disarticulated.
4. Less than 25% full.	Cuticle broken into small fragments.
5. Empty.	Empty.

Stomach contents with a digestion state of 1 were seldom found in the DSB III samples but were rather common in the Teuthis material, probably because of feeding in the trawl.

Table 5 shows the kind and number of food items found in the stomachs of each species. Often the stomach contents were too well digested for identification. Food items were not identified beyond the general categories presented except for the calanoid copepod genus *Pleuromamma*, which has a prominent shiny knob on the side of the metasome that is highly resistant to digestion.

RESULTS

Sergestid species occurring in Hawaiian waters are listed in Table 6, along with the total number caught. *Sergestes* and *Sergia* until recently were considered to be subgenera of genus *Sergestes* s.l.; however, Omori (1974) has rightly elevated the subgenera to full genera. This paper follows his usage but gives feminine endings to species of *Sergia*. A paper presenting systematic descriptions of Hawaiian species is in preparation.

Sergestes atlanticus Milne Edwards 1830

Vertical Distribution (Figure 1)

The normal daytime range of *S. atlanticus* was 550 to 725 m. Small individuals had a more restricted range than the larger ones; shrimp less than 5.5 mm CL stayed between 550 and 650 m. *Sergestes atlanticus* was occasionally taken at 800 m or below. The small concentrations between 800 and 1,050 m in Figure 1 all resulted from the June 1973 cruise. In addition, the December 1970 cruise took seven shrimp in an 800-m tow. At night *S. atlanticus* occurred over a wide range from the surface to about 300 m. The large concentration in the upper 25 m resulted from a single large capture in May 1973. This depth interval was extensively sampled by only three tows, so it is unclear

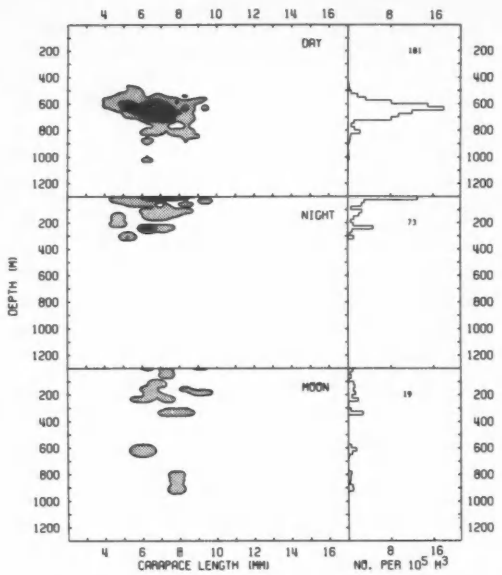

FIGURE 1.–Vertical distribution of *Sergestes atlanticus*.

whether the bulk of the population normally occurs so shallow. A number of night tows in the 75- to 150-m range took small numbers of *S. atlanticus*, and one tow at about 250 m captured five individuals. There appeared to be no significant variation of depth with size. Tows on moonlit nights took small numbers of *S. atlanticus* from the surface to about 350 m, with a possible concentration around 150-175 m. Several captures were made between 600 and 925 m, suggesting that at least part of the population did not always migrate. The December 1970 cruise took substantial numbers (up to seven) near full moon between 250 and 300 m, and also between 550 and 800 m, indicating that only part of the population was migrating. Later in the cruise when the moon was waning, tows between 30 and 100 m took *S. atlanticus* in moderate numbers (four to six).

Population Size, Growth, and Reproduction (Figure 2)

Sergestes atlanticus was moderately abundant, turning up regularly in tows at the appropriate

TABLE 3.–Estimated population sizes of Hawaiian sergestids from all horizontal tows and two series of oblique tows (no. per 100 m²).

Species	Teuthis XVIII				Teuthis XXII				Horizontal		
	(1)	$\bar{x}$	s	n	(1)	$\bar{x}$	s	n	(1)	$\bar{x}$	n
Sergestes atlanticus	DD	4.36	3.66	28	DD	1.17	1.67	9	D	2.10	180
	DN	2.66	1.31	19	DN	1.10	1.47	6	N	0.84	68
	SN	4.28	3.09	47	SN	0.28	0.56	2	M	0.46	19
		3.79	2.75	94		0.88	1.33	17		1.31	267
Sergestes erectus	DD	7.22	3.06	45	DD	1.79	1.25	13	D	5.55	542
	DN	5.30	3.83	39	DN	1.91	1.00	10	N	2.02	156
	SN	5.46	2.61	59	SN	2.28	0.80	16	M	2.83	151
		5.85	3.03	143		1.97	1.01	39		3.81	849
Sergestes armatus	DD	12.37	14.47	73	DD	1.18	1.85	8	D	2.48	251
	DN	12.16	7.69	84	DN	1.46	1.70	8	N	2.63	141
	SN	7.61	3.61	83	SN	0.87	0.80	6	M	1.83	41
		10.22	8.28	250		1.15	1.45	22		2.35	433
Sergestes vigilax	DD	3.33	2.52	20	DD	0.76	0.96	6	D	0.52	57
	DN	2.30	1.55	17	DN	0.72	0.81	4	N	0.28	30
	SN	4.63	1.42	50	SN	0.99	0.83	2	M	0.15	13
		3.58	1.95	87		0.61	0.75	12		0.35	100
Sergestes orientalis	DD	5.54	4.12	34	DD	0.65	0.92	5	D	1.61	160
	DN	5.11	2.00	38	DN	0.18	0.31	1	N	1.39	130
	SN	12.45	5.03	130	SN	0.99	0.83	7	M	0.75	42
		8.43	5.29	202		0.64	0.80	13		1.32	332
Sergestes consobrinus	DD	6.72	3.70	42	DD	2.48	1.42	18	D	0.72	81
	DN	3.30	1.28	24	DN	2.10	1.96	11	N	1.99	231
	SN	5.82	4.13	63	SN	1.45	1.03	10	M	0.57	13
		5.26	3.46	129		2.08	1.40	39		1.05	325
Sergestes sargassi	DD	10.37	7.85	68	DD	1.55	1.41	11	D	0.64	71
	DN	3.53	1.40	25	DN	1.68	0.95	9	N	1.07	77
	SN	4.91	2.16	52	SN	2.06	1.60	15	M	0.40	26
		5.84	4.73	145		1.74	1.29	35		0.70	174
Sergestes pectinatus	DD	23.24	17.36	141	DD	6.95	4.04	51	D	2.01	245
	DN	24.14	14.13	178	DN	2.58	1.34	14	N	1.54	136
	SN	30.44	20.86	330	SN	2.89	2.04	21	M	1.40	86
		26.67	17.30	649		4.70	3.59	86		1.71	467

TABLE 3.—Continued.

Species	Teuthis XVIII (1)	$\bar{x}$	s	n	Teuthis XXII (1)	$\bar{x}$	s	n	Horizontal (1)	$\bar{x}$	n
Sergia fulgens	DD	0.35	0.69	2	DD	24.15	19.01	186	D	1.55	185
	DN	0.29	0.40	2	DN	8.63	4.17	46	N	2.21	237
	SN	0.63	0.60	12	SN	9.15	5.08	64	M	3.57	134
		0.45	0.55	16		15.95	14.91	296		2.26	556
Sergia scintillans	DD	9.86	8.55	40	DD	5.12	4.41	39	D	3.69	355
	DN	6.80	5.17	51	DN	0.72	0.81	4	N	3.59	329
	SN	12.14	6.95	130	SN	3.80	2.17	27	M	2.35	151
		9.90	6.83	221		1.90	2.25	70		3.31	835
Sergia gardineri	DD	8.80	2.13	55	DD	5.12	4.41	17	D	11.22	964
	DN	11.74	9.23	88	DN	0.72	0.81	15	N	9.95	793
	SN	9.44	3.88	100	SN	0.56	0.45	4	M	2.67	51
		10.00	5.58	243		1.90	2.25	36		8.65	1,808
Sergia bigemmea	DD	2.50	2.04	16	DD	0.29	0.45	2	D	0.37	27
	DN	3.19	2.57	23	DN	0.76	0.84	4	N	1.48	116
	SN	1.67	0.95	18	SN	0.00	0.00	0	M	0.19	2
		2.35	1.85	57		0.31	0.53	6		0.64	145
Sergia inequalis	DD	2.01	1.76	12	DD	0.38	0.63	3	D	0.63	16
	DN	0.61	1.37	5	DN	0.57	0.56	3	N	0.76	50
	SN	0.57	0.60	6	SN	0.00	0.00	0	M	0.19	10
		0.94	1.29	23		0.31	0.52	6		0.55	76
Sergia bisulcata	DD	1.15	1.09	7	DD	1.03	1.19	8	D	1.04	91
	DN	1.31	1.76	9	DN	0.37	0.64	2	N	1.32	68
	SN	1.12	0.48	12	SN	0.82	0.90	6	M	1.96	38
		1.19	1.08	28		0.82	0.96	16		1.35	197
Sergia tenuiremis	DD	0.43	0.52	3	DD	0.77	0.97	6	D	0.93	39
	DN	0.86	1.17	6	DN	0.55	0.96	3	N	0.99	25
		0.67	0.91	9		0.70	0.91	9	M	0.73	14
										0.89	78
Petalidium suspiriosum	DD	1.09	0.73	7	DD	1.50	2.29	10	D	1.94	53
	DN	1.30	1.09	9	DN	0.93	0.58	5	N	0.82	13
		1.21	0.90	16		1.31	1.85	15	M	2.84	22
										1.84	88

(1) DD—Deep Day tows (0-1,200 m): T18 four tows, T22 six tows.
DN—Deep Night tows (0-1,200 m): T18 five tows, T22 three tows.
SN—Shallow Night tows (0-400 m): T18 seven tows, T22 five tows.
D—DAY Horizontal tows.
N—NIGHT Horizontal tows.
M—MOON Horizontal tows.

TABLE 4.—Feeding chronology of sergestids from DSB III.

Species	DAY (Tow no. 1-3, 12) Number examined	Empty (%)	Content[1]	Digestion[1]	NIGHT (Tow no. 5-10) Number examined	Empty (%)	Content[1]	Digestion[1]
Sergestes atlanticus	0	—	—	—	2	0	1.5	3.5
Sergestes erectus	12	17	3.7	3.9	38	26	3.3	3.8
Sergestes armatus	11	82	4.8	4.7	20	65	3.7	4.3
Sergestes vigilax	0	—	—	—	1	100	5.0	5.0
Sergestes orientalis	1	100	5.0	5.0	1	0	3.0	4.0
Sergestes sargassi	0	—	—	—	10	30	3.5	4.0
Sergestes pectinatus	0	—	—	—	9	22	2.7	3.6
Sergia fulgens	2	50	4.0	4.5	6	67	4.1	4.2
Sergia scintillans	0	—	—	—	29	18	2.8	3.8
Sergia gardineri	3	67	3.7	4.1	8	37	3.2	4.2
Sergia bigemmea	2	0	3.0	4.0	76	11	3.0	3.6
Sergia inequalis	0	—	—	—	1	0	4.0	3.5
Sergia bisulcata	2	0	3.2	4.0	5	20	3.0	3.6
Sergia tenuiremis	1	100	5.0	5.0	0	—	—	—
Total sample	34	62	4.1	4.2	205	22	3.1	3.7

[1] See text.

depths, but seldom in numbers greater than five or six for a 3-h tow. The average population density estimated from all horizontal tows was 1.31 per 100 m^2. Daytime tows caught larger numbers than nighttime tows, the population density from daytime horizontal tows being 2.10 per 100 m^2. The

TABLE 5.—Diet of sergestids from DSB III.

Number of shrimp containing	*Sergestes atlanticus*	*Sergestes erectus*	*Sergestes armatus*	*Sergestes vigilax*	*Sergestes orientalis*	*Sergestes sargassi*	*Sergestes pectinatus*	*Sergia fulgens*	*Sergia scintillans*	*Sergia gardineri*	*Sergia bigemmea*	*Sergia inequalis*	*Sergia bisulcata*	*Sergia tenuiremis*
Calanoid copepods	1	27	6			3	7	1	7	2	23	1		
Pleuromamma[1]	1	8	1			1	5		2		3			
Cyclopoid copepods									3		6			
Amphipods	1	3	3					1	3		6		1	
Ostracods					1			1	1	1	15		2	
Euphausiids		1	1			1							1	
Decapod larvae			1						1	1	1		1	
Bivalve larvae	1							1	18	1	16		1	
Foraminifera								3	10	2	4		1	
Chaetognath spines											3			
Unidentified crustacea		19	1			3	3	1	17	3	33		3	
Fibrous matter									5		2		1	
Other[2]	1	1						1	5	1	4			
Empty		17	29	1	1	3	2	2	5	13	11		1	3
Total number examined	3	62	41	1	2	10	12	9	35	19	88	1	8	3

[1]Included with calanoid copepods.
[2]Including gastropod larvae, radiolarians, pteropods, fish eggs, and fish scales.

TABLE 6.—Numbers of Hawaiian sergestids captured, 1970-73.

Half-red species	
Sergestes atlanticus Milne-Edwards	546
Sergestes cornutus Krøyer	17
Sergestes erectus Burkenroad	1,371
Sergestes armatus Krøyer	1,113
Sergestes vigilax Stimpson	271
Sergestes orientalis Hansen	1,030
Sergestes tantillus Burkenroad	21
Sergestes consobrinus Milne	647
Sergestes sargassi Ortmann	497
Sergestes pectinatus Sund	1,541
Sergia fulgens (Hansen)	1,118
Sergia scintillans (Burkenroad)	1,610
All-red species	
Sergia gardineri (Kemp)	3,096
Sergia bigemmea (Burkenroad)	398
Sergia inequalis (Burkenroad)	149
Sergia bisulcata (Wood-Mason)	350
Sergia maxima (Burkenroad)	2
Sergia tenuiremis (Krøyer)	147
Petalidium suspiriosum Burkenroad	170

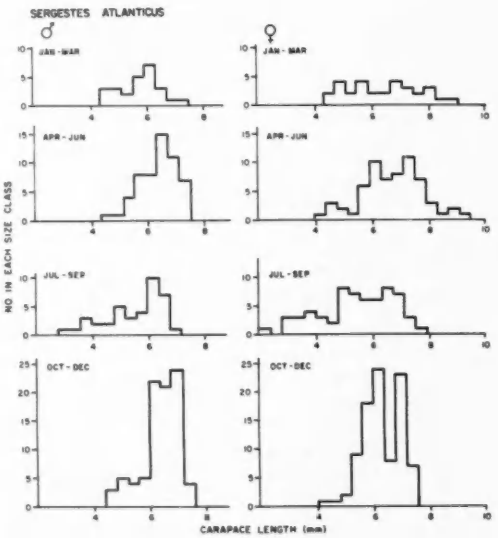

FIGURE 2.—Quarterly size-frequency distribution of *Sergestes atlanticus*.

September 1972 oblique series gave a figure of 3.79 per 100 m^2, and the May 1973 oblique series yielded 0.88 per 100 m^2; these figures are probably close to the maximum and minimum population density.

Recruitment was highest during the third quarter (July-September), the only time of year when immature shrimp less than 4 mm CL were taken. The largest shrimp were most abundant during the second quarter (April-June).

Diet (Table 5)

Only three individuals examined had recognizable stomach contents: a calanoid copepod (*Pleuromamma*), an amphipod, and fragments of larval bivalve shells.

Sergestes cornutus Krøyer 1855

Vertical Distribution

Only four individuals were captured in horizon-

tal closing tows; these were all daytime tows between 450 and 550 m. Several were captured in 0- to 400-m oblique night tows, indicating that *S. cornutus* is a vertical migrator. Donaldson (1975) found *S. cornutus* mostly in the upper 50 m at night.

Population structure and diet were not studied because of the small sample size.

Sergestes erectus Burkenroad 1940

Vertical Distribution (Figure 3)

Sergestes erectus was abundant in our collection, but nearly half of the shrimp came from daytime tows of the November 1972 cruise. The daytime vertical range was about 550 to 800 m, with maximum catches between 625 and 750 m. Immature shrimp did not occur below 750 m. The nighttime range varied with size. Small immature shrimp less than 12 mm CL occurred between the surface and 200 m, mostly below 125 m. Intermediate-sized shrimp between 12 and 16 mm CL, including immature and newly mature shrimp, ranged between 150 and 250 m. Adult shrimp larger than 16 mm CL were found between 250 and 325 m. Moonlight depressed the vertical range of adults very little, although there were some captures in the 350- to 475-m range; immatures were found between 175 and 250 m. The peak in the upper 25 m is a sampling artifact. There was no positive evidence of full moon nonmigration in the horizontal samples, but the December 1970 cruise took a dozen shrimp in the 575- to 700-m range, suggesting that about 20-30% of the population was not migrating.

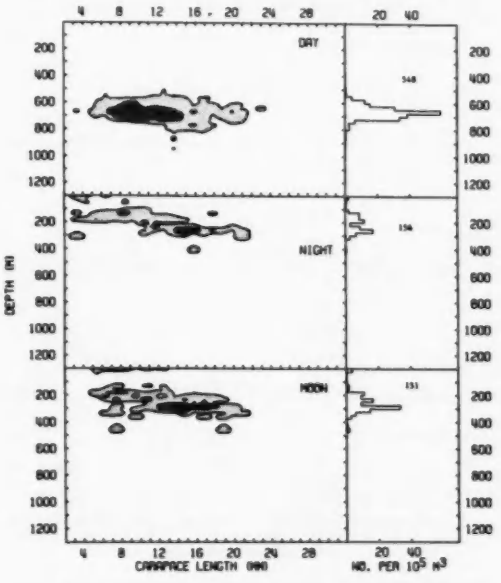

FIGURE 3.–Vertical distribution of *Sergestes erectus*.

Population Size, Growth, and Reproduction (Figure 4)

Sergestes erectus was the second most abundant species in the horizontal series, the average population density estimated from all horizontal tows amounting to 3.81 per 100 m^2. Like *S. atlanticus*, it was taken in larger numbers during the daytime than at night, the population density estimated from daytime horizontal tows amounting to 5.55 per 100 m^2. These numbers reflect its extreme abundance during the November 1972 cruise, when as many as 157 were taken in a single 3-h tow. The oblique series of September 1972 and

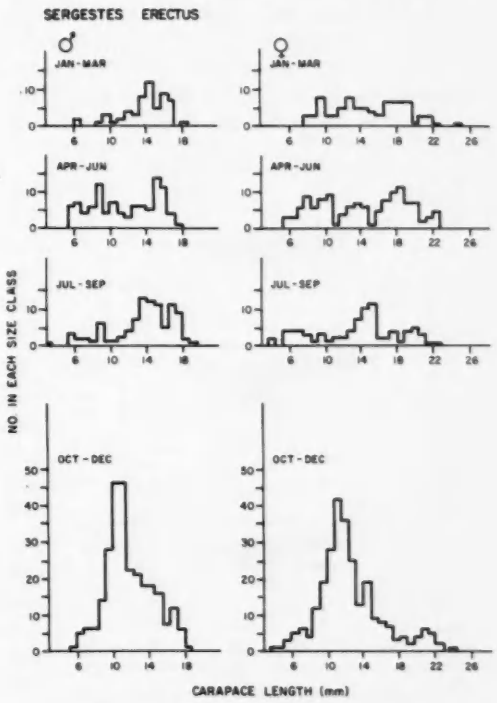

FIGURE 4.–Quarterly size-frequency distribution of *Sergestes erectus*.

May 1973 yielded figures of 5.85 and 1.97 per 100 m^2, respectively.

Recruitment was not noticeably high during any particular quarter. However, medium-sized shrimp in the 10- to 14-mm CL range were significantly more abundant during the fourth quarter (October-December) than at other times of the year (Kolmogorov-Smirnov test, $P<0.05$).

Diet (Table 5)

Calanoid copepods made up the bulk of the stomach contents of the *S. erectus* from DSB III. A few amphipods and a single euphausiid were also found. One individual had some material very tentatively identified as a small fish, the only one found in the DSB III collection. No food items in the 0.4- to 0.6-mm size range were found.

Sergestes armatus Kröyer 1855

Vertical Distribution (Figure 5)

The daytime vertical distribution of *S. armatus* varied somewhat with size. Immature shrimp ranged between 450 and 600 m; adults were generally between 550 and 650 m, but sometimes as shallow as 450 m. One tow in November 1972 took 13 shrimp at about 675 m. The December 1970 cruise took nine shrimp in open tows below 800 m; most of these were probably contaminants. The nighttime range also varied with size; shrimp smaller than 8 mm CL usually occurred between 100 and 200 m, while adults were found mostly between 150 and 300 m, with occasional captures as deep as 450 m. Moonlight did not depress the vertical distribution of *S. armatus*. The peak in the upper 25 m is a sampling artifact. The open tows of the December 1970 and December 1973 cruises took small to moderate numbers of *S. armatus* at the daytime depth. If these shrimp were not contaminants, they suggest that about 5-20% of the December 1973 population was not migrating.

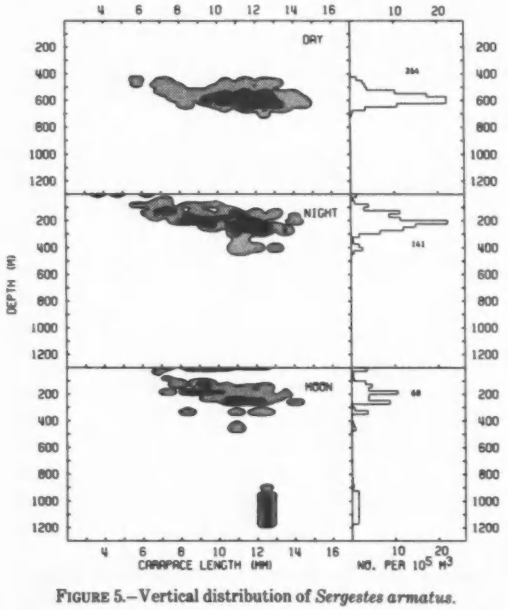

FIGURE 5.—Vertical distribution of *Sergestes armatus*.

Population Size, Growth, and Reproduction (Figure 6)

Sergestes armatus was abundant in the horizontal series, the average population density of 2.35 per 100 m^2 estimated from all horizontal tows making it the fourth most abundant sergestid. The catch was even greater during the September 1972 oblique series, which yielded a figure of 10.22 per 100 m^2, second only to *S. pectinatus*. The May 1973 oblique series took much smaller numbers, amounting to only 1.51 per 100 m^2.

Recruitment was much higher during the second quarter (April-June) than during the rest of the year. Large individuals were most abundant during the fourth quarter (October-December).

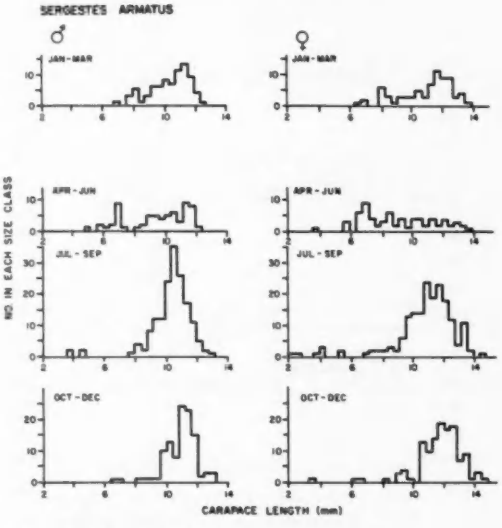

FIGURE 6.—Quarterly size-frequency distribution of *Sergestes armatus*.

Diet (Table 5)

DSB III took over 40 *S. armatus*, but two-thirds had empty stomachs. Food items included calanoid copepods, amphipods, an euphausiid, and an unidentified decapod larva. Prey in the 0.4- to 0.6-mm size range, such as foraminifera or bivalve larvae, were not found.

Sergestes vigilax Stimpson 1860

Vertical Distribution (Figure 7)

The daytime vertical range of *S. vigilax* was about 550 to 725 m, with a concentration at about 675 m. Nighttime captures were all in the 0- to 200-m depth range, peaking at about 50-75 m. Moonlight depressed the peak to 150-200 m, but some individuals remained shallower. There was no evidence of full moon nonmigration.

Population Size, Growth, and Reproduction (Figure 8)

Sergestes vigilax was not abundant in Hawaiian waters. The average population density estimated from all horizontal tows was only 0.35 per 100 m^2. Daytime catches were larger than night catches, the population estimate from the day tows being 0.52 per 100 m^2. The oblique series of September 1972 and May 1973 took larger numbers, yielding estimates of 3.57 and 0.61 per 100 m^2, respectively. These larger population sizes may indicate that the finer mesh of the IKMT sampled *S. vigilax*, a relatively small species, more efficiently than did the MT used for the horizontal tows.

The seasonal size-frequency histograms are not significantly different from one another. Shrimp less than 5 mm CL were most abundant in the third quarter (July-September).

Diet (Table 5)

Only a single individual was examined; it had an empty stomach.

Sergestes orientalis Hansen 1919

Vertical Distribution (Figure 9)

The daytime vertical distribution of *S. orientalis* varied with size; small shrimp less than 6.5 mm CL were taken from 450 to 575 m, while larger ones were found between 500 and 625 m, mostly between 550 and 600 m. The nighttime range was from the surface to 125 m, with largest numbers in the 25- to 50-m and 75- to 100-m zones. Small shrimp less than 6 mm CL stayed above 75 m. Moonlight depressed most of the nighttime

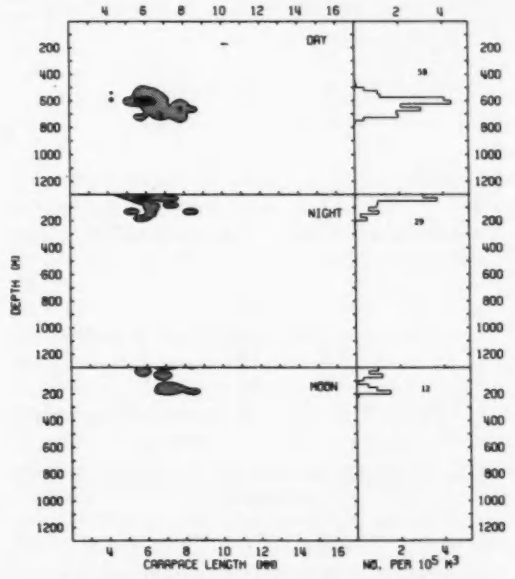

FIGURE 7.–Vertical distribution of *Sergestes vigilax*.

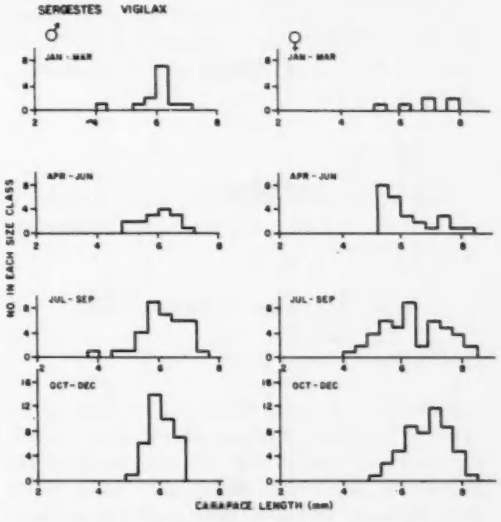

FIGURE 8.–Quarterly size-frequency distribution of *Sergestes vigilax*.

population into the 100- to 200-m range, although some remained shallower. A few nighttime captures were made in the daytime depth range. The December 1970 cruise took large numbers near full moon at 550-600 m (up to 40), and also at 150-200 m (up to 21). Apparently at least 50% of the population was not migrating. Later in the cruise, when the moon was waning, large numbers of *S. orientalis* were taken in tows between 30 and 120 m (up to 70). There was no evidence of full moon nonmigration during the December 1973 cruise.

Population Size, Growth, and Reproduction (Figure 10)

Sergestes orientalis was moderately abundant in Hawaiian waters. The average population density estimated by all the horizontal tows was 1.32 per 100 m^2, daytime and night tows giving similar figures. The oblique series of September 1972 yielded a higher figure of 8.43 per 100 m^2, *S. orientalis* being the second most abundant species in the shallow night tows. On the other hand, it was much scarcer during the oblique series of May 1973, which gave a population density of only 0.64 per 100 m^2. *Sergestes orientalis* was particularly abundant during the December 1970 cruise, when as many as 70 were taken in a single 3-h IKMT tow.

The seasonal size-frequency histograms are all very similar to one another. Shrimp smaller than 6 mm CL were proportionally most abundant during the first quarter (January-March), but the difference was not statistically significant (Kolmogorov-Smirnov test, $P > 0.05$).

Diet (Table 5)

Only two individuals from DSB III were examined. One had an empty stomach; the other had eaten an ostracod.

Sergestes tantillus Burkenroad 1940

Vertical Distribution

Because of the rarity of *S. tantillus*, little can be inferred about its vertical distribution. Single shrimp were taken in daytime tows between 410 and 915 m. The largest night catch was at 50 m (four shrimp), with individual captures to about 200 m. A tow between 635 and 715 m on a moonlit night took six shrimp.

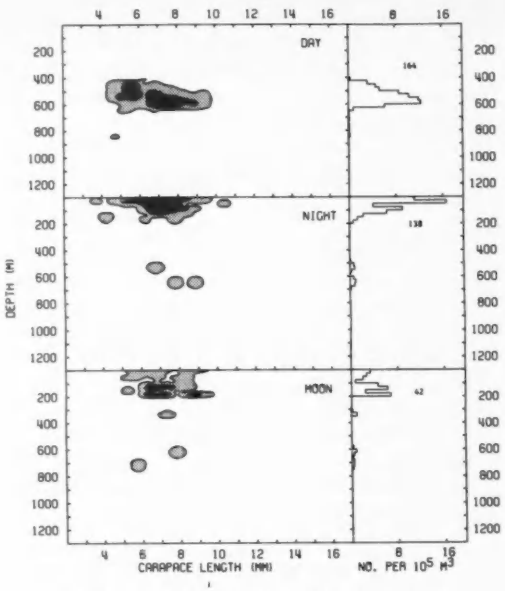

FIGURE 9.–Vertical distribution of *Sergestes orientalis*.

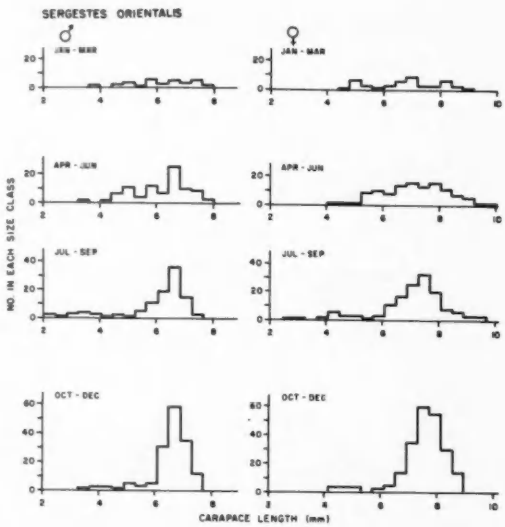

FIGURE 10.–Quarterly size-frequency distribution of *Sergestes orientalis*.

Growth, reproduction, and diet were not studied because of the small sample size.

Sergestes consobrinus Milne 1968

Vertical Distribution (Figure 11)

Nearly two-thirds of the captures during the Teuthis series were from shallow night tows during the May 1973 cruise (Teuthis XXI); it was also fairly abundant in the oblique series of September 1972 and May 1973 (Teuthis XXII).

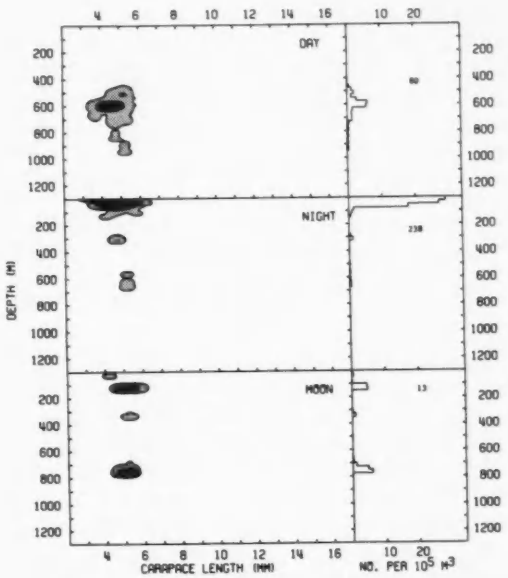

FIGURE 11.–Vertical distribution of *Sergestes consobrinus*.

Sergestes consobrinus was broadly distributed during the daytime, from 450 to 725 m. The population maximum appeared to be around 600 m, but most daytime catches were small. A few captures were made between 800 and 950 m; these may have been contaminants. The nighttime distribution showed a broad peak from the surface to 75 m, with lesser numbers to 125 m. These numbers were strongly influenced by the May 1973 captures. Moonlight depressed most of the population to 100-150 m, with a substantial number remaining at the daytime depth. The December 1970 cruise took *S. consobrinus* near full moon in tows between 140 and 180 m, and also in a 700- to 800-m tow. Later catches when the moon was waning were in the upper 120 m, with a large catch at 30 m.

Population Size, Growth, and Reproduction (Figure 12)

Like *S. vigilax*, *S. consobrinus* appears to have been undersampled by the MT. The average population size estimated by all horizontal tows was 1.05 per 100 m^2. The figure for only the night tows was 1.99 per 100 m^2, reflecting the large night catches of the May 1973 cruise (Teuthis XXI)–up to 76 in a single 3-h tow. The oblique IKMT series of September 1972 and May 1973 (Teuthis XXII) yielded higher figures of 5.42 and 2.08 per 100 m^2, respectively, presumably because the finer mesh of the IKMT retained more of the small shrimp.

The seasonal size-frequency histograms show a maximum proportion of small individuals in the third quarter (July-September). The largest shrimp were taken in the first and second quarters, although first quarter catches were small.

Diet was not examined, since none were taken during DSB III.

Sergestes sargassi Ortmann 1893

Vertical Distribution (Figure 13)

With the possible exception of *S. cornutus*,

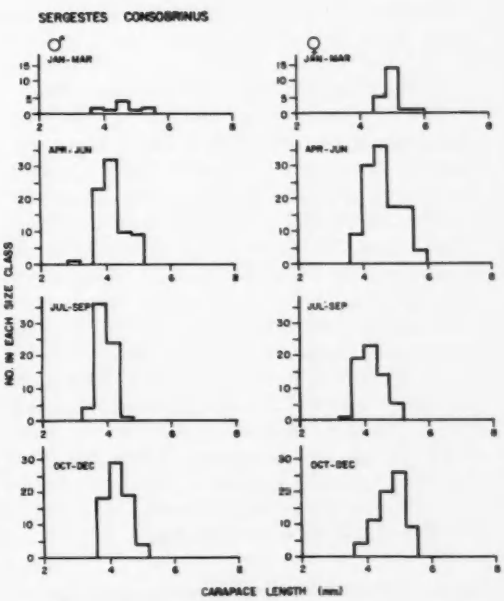

FIGURE 12.–Quarterly size-frequency distribution of *Sergestes consobrinus*.

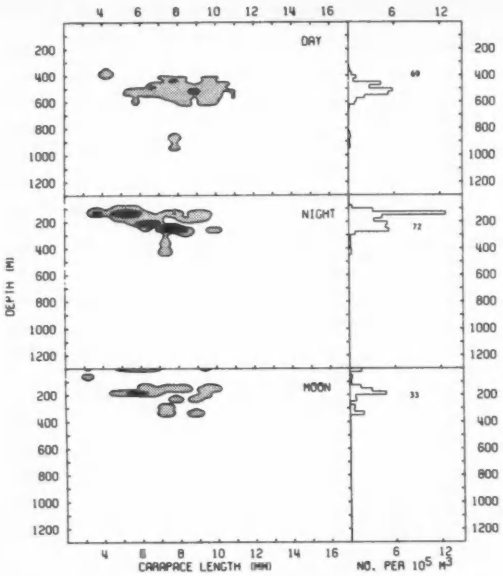

FIGURE 13.–Vertical distribution of *Sergestes sargassi*.

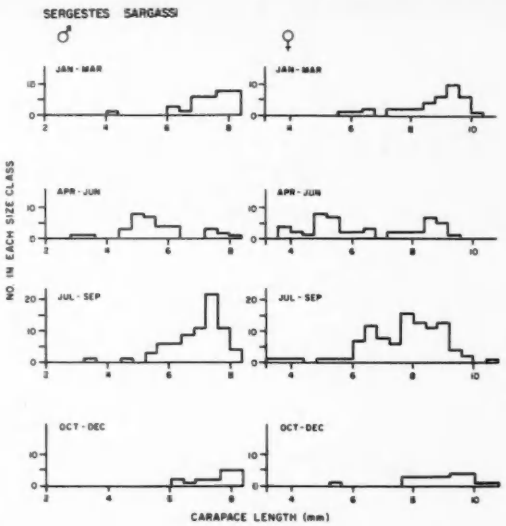

FIGURE 14.–Quarterly size-frequency distribution of *Sergestes sargassi*.

which is very rare in Hawaiian waters, *S. sargassi* had the shallowest daytime range of the local species: 450-575 m, with a maximum around 475 m. No significant variation of depth with size was noted, perhaps because of the small number caught. One immature shrimp was captured between 340 and 425 m, and oblique tows from the surface to about 350 m took a few immature specimens in September 1972. There was a pronounced variation of size with depth at night. Immature individuals less than 6 mm CL occurred between 100 and 200 m, mostly in the 125- to 150-m range. Larger shrimp were found from 125 to 300 m, mostly from 225 to 275 m. Most of the adults captured at night were males; the few females were mostly taken between 125 and 175 m. This apparent segregation by sex was probably a sampling artifact, since the December 1970 cruise took both males and females in tows from 250 to 300 m. Moonlight had little effect on the depth range of adults; immature individuals were depressed to about 150-200 m. The peak in the upper 25 m is a sampling artifact. There was no evidence of full moon nonmigration.

Population Size, Growth, and Reproduction (Figure 14)

Sergestes sargassi was not very abundant in the horizontal collections, the estimated average population density being only 0.70 per 100 m^2. The night tows gave a higher total than the daytime tows, 1.07 and 0.64 per 100 m^2, respectively. The two IKMT oblique series of September 1972 and May 1973 produced higher estimates, 5.84 and 1.74 per 100 m^2, respectively; the daytime figure of 10.37 per 100 m^2 in September was the third highest such total for that cruise. These higher figures for the IKMT tows were not the result of more efficient filtering, as appears to be the case for the smaller species, since *S. sargassi* is a moderately large species, about the same size as *Sergia scintillans* and *Sergia gardineri*, neither of which showed any signs of significant undersampling by the MT.

Recruitment was highest during the second quarter (April-June), when nearly 70% of the population was immature. Growth during the summer was about 1.0-1.3 mm CL per month, slowing during the third and fourth quarters to 0.2-0.5 mm CL per month. Maximum sizes were attained in December and the first quarter (January-March).

Diet (Table 5)

DSB III took 10 *S. sargassi*. Three had empty stomachs. The rest had eaten zooplanktonic

crustacea, including calanoid copepods and a euphausiid.

Sergestes pectinatus Sund 1920

Vertical Distribution (Figure 15)

The daytime range of *S. pectinatus* was broad, extending from 425 to 725 m. The peak at 425-450 m came from a single tow in the June 1971 cruise, and the peak at 650-675 m was also from a single tow in the November 1972 cruise. Most large catches centered around 575 to 625 m. There was a poorly defined size-depth trend. Small shrimp less than 4 mm CL seldom occurred below 600 m, while the very large females seldom occurred above 550 m. At night the size-depth trend was pronounced. Males less than 3.5 mm CL were found in the upper 100 m, mostly between 25 and 75 m. From 4 to 5 mm CL, maximum catches were in the 75- to 250-m range, peaking around 150 m. The largest males were taken in the 200- to 275-m range. Females showed a similar trend; maximum catches of shrimp less than 4.5 mm CL occurred around 50 m, increasing to 150 m for shrimp between 4.5 and 6 mm CL, and 200 m for shrimp larger than 6 mm CL. A few shrimp were taken below 300 m; these may have been contaminants. The moon depressed most of the population to about 150-250 m. The peak in the upper 25 m is a sampling artifact. None of the Teuthis samples showed any indications of full moon nonmigration. The December 1970 cruise took 14 specimens in three open tows between 400 and 600 m, probably representing less than 10% of the population.

Population Size, Growth and Reproduction (Figure 16)

Sergestes pectinatus appeared to be significantly undersampled by the MT. The average population density estimated by all horizontal tows was 1.71 per 100 m^2. The IKMT with its finer mesh captured many more shrimp than the MT. *Sergestes pectinatus* was the most abundant sergestid in the September 1972 oblique series, which yielded a population density estimate of 26.67 per 100 m^2. The shrimp from this cruise composed nearly 40% of the entire catch of *S. pectinatus*. The May 1973 series gave a figure of 4.70 per 100 m^2, second only to *S. fulgens*. In both cases, the average size of an individual was considerably smaller than in a typical MT tow. Interpretation of the size-frequency histograms is complicated by the undersampling problem. For *S. pectinatus* only, data from the May 1973 oblique series were added to the second quarter horizontal data. This means

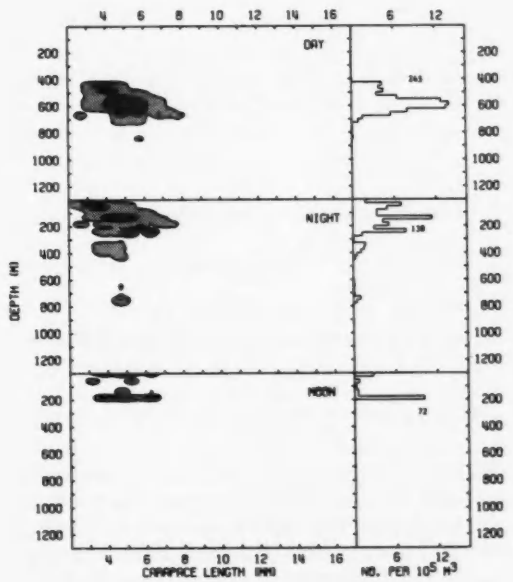

FIGURE 15.—Vertical distribution of *Sergestes pectinatus*.

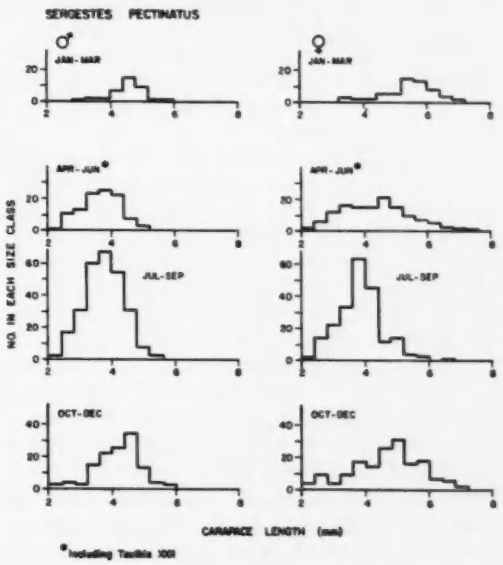

FIGURE 16.—Quarterly size-frequency distribution of *Sergestes pectinatus*. April-June quarter includes data from Teuthis XXII.

that IKMT data were included in three of the four quarters, only the first quarter (January-March) lacking IKMT data. Small shrimp were proportionately most abundant during the third quarter (July-September), and large shrimp were most abundant during the first quarter, although lack of IKMT data probably affected the shape of the first quarter histogram.

Diet (Table 5)

Seven of the twelve shrimp from DSB III had eaten calanoid copepods, mostly *Pleuromamma* spp.

Sergia fulgens (Hansen 1919)

Vertical Distribution (Figure 17)

Because of the peculiar fluctuations in abundance during the course of the sampling program, the vertical distribution patterns of *S. fulgens* derived from the data should be regarded strictly as estimates. All the daytime captures lay between 550 and 625 m; there was no variation in depth with increasing size. The open tows of the December 1970 cruise took nine specimens between 525 and 630 m. Most nighttime captures lay between 75 and 125 m for immature shrimp less than 8 mm CL, with some as shallow as 25-50 m. Nearly all the adults came from a single tow at 150-200 m; a few captures came as shallow as 75 m. Almost all of the captures near full moon came during the June 1973 cruise, which took immature shrimp between 250 and 475 m; there were three captures of adults between 150 and 325 m. The peak in the upper 25 m is a sampling artifact. The December 1970 cruise took nine adults in open tows between 160 and 300 m and one adult at 400 m. There was no evidence of full moon nonmigration.

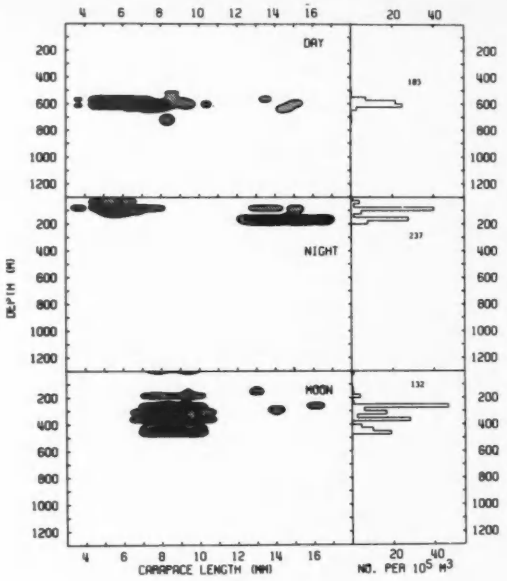

FIGURE 17.–Vertical distribution of *Sergia fulgens*.

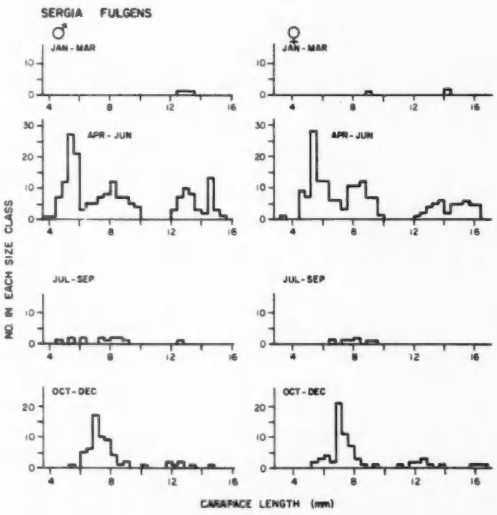

FIGURE 18.–Quarterly size-frequency distribution of *Sergia fulgens*.

Population Size, Growth, and Reproduction (Figure 18)

Sergia fulgens fluctuated drastically in abundance during the sampling program. The first 13 cruises of the Teuthis series (Teuthis IV-XVII, February 1971-August 1972) caught a total of 13 specimens. After the September 1972 cruise it turned up in many tows, often in very large numbers. Nearly all the specimens were immature shrimp less than 10 mm CL. However, one horizontal night tow in May 1973 took 89 adults. In addition, the December 1970 cruise caught a total of 21 *S. fulgens*; 19 of these were adults. Combining the very low numbers from the first 13 horizontal series with the very high numbers from the last 3 horizontal series gives an average population

density of 2.26 per 100 m^2, an estimate of doubtful meaning. The two oblique series produced very different estimates. The September 1972 cruise gave a figure of only 0.43 per 100 m^2, making *S. fulgens* the least abundant of the 16 regularly occurring species. On the other hand, the May 1973 cruise gave a figure of 15.95 per 100 m^2, more than 3 times greater than any other species, and 37 times the September figure.

The seasonal size-frequency histograms reflect the fact that nearly all *S. fulgens* were caught in the second and third quarters. The second quarter (April-June) histogram is trimodal. The peaks at 5.5 and 8 mm CL represent the same cohort as sampled in May and June (the Teuthis XXII oblique series of late May took 6.5-mm shrimp), giving a growth rate of 2.1-2.2 mm CL per month for immature shrimp in this size range. The assumption that the peak at 13-15 mm in May is the same cohort as the peak at 7.5 mm from the preceding November yields a growth rate of 1.0-1.2 mm CL per month, reflecting a slowing of the growth rate as the shrimp approach maturity. The presence of large numbers of immature shrimp in the second and fourth quarters implies that *S. fulgens* either has a very broad spawning period or has two widely separated spawning peaks.

Diet (Table 5)

DSB III took nine *S. fulgens*. Seven of these had food in their stomachs, including a calanoid copepod, an amphipod, and an ostracod, plus smaller prey including larval bivalve and foraminifera.

Sergia scintillans (Burkenroad 1940)

Vertical Distribution (Figure 19)

The vertical distribution of *S. scintillans* showed a slight tendency for smaller shrimp to live deeper than larger ones, both day and night. Daytime ranges were about 575 to 700 m for individuals less than 7 mm CL and 525 to 650 m for those larger than 7 mm CL, with maximum catches between 575 and 625 m. The small peak at 325-350 m resulted from two shrimp taken in a tow that dipped as deep as 480 m; they were probably captured at the deep end of the tow. At night the adults were mostly between 25 and 125 m, but immature shrimp less than 6 mm CL ranged

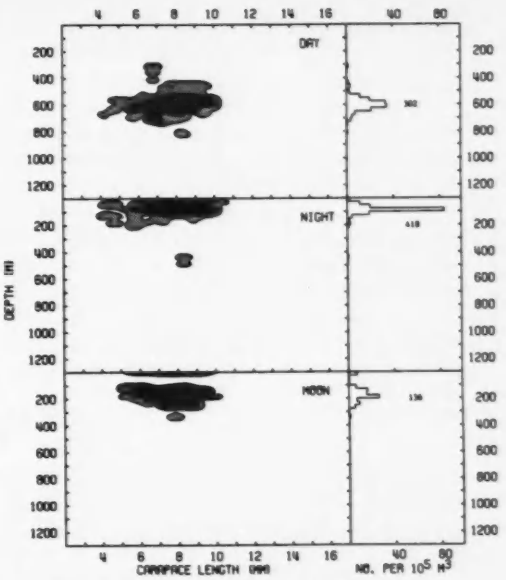

FIGURE 19.—Vertical distribution of *Sergia scintillans*.

between 50 and 225 m. Although the population was centered at 100-125 m for both sexes, few males occurred shallower than 50 m. Three shallow tows from the May 1973 cruise that caught 40 females and 12 males are primarily responsible for this difference. Moonlight depressed the depth of most of the population to 100-275 m, peaking around 200 m. The peak in the upper 25 m is a sampling artifact. There was no evidence of full moon nonmigration.

Population Size, Growth, and Reproduction (Figure 20)

Sergia scintillans was one of the most abundant sergestids in Hawaiian waters. The average population density estimated by all horizontal tows was 3.31 per 100 m^2, the daytime and nighttime figures being similar. It was particularly abundant in the shallow night tows of the May 1973 cruise (Teuthis XXI), one 3-h tow taking 179 shrimp. The oblique series of September 1972 and May 1973 (Teuthis XXII) produced figures of 9.90 and 3.70 per 100 m^2, respectively.

Small shrimp were proportionally most abundant in the third quarter (July-September). First and second quarter populations were similar in size-frequency, although the larger females occurred in the second quarter (April-June).

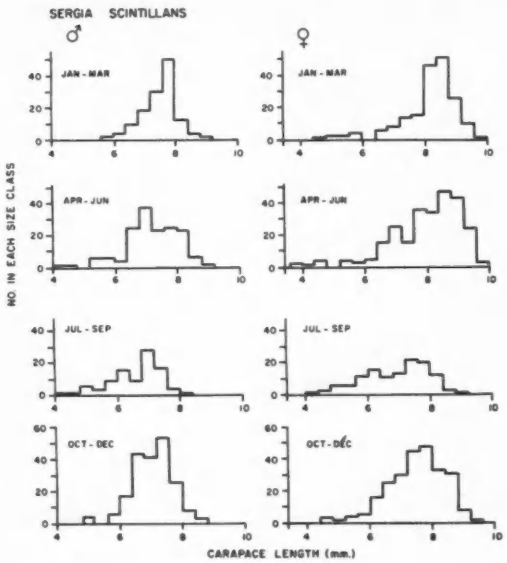

FIGURE 20.–Quarterly size-frequency distribution of *Sergia scintillans*.

Diet (Table 5)

The DSB III material showed that *S. scintillans* ate the usual variety of zooplanktonic crustacea, including calanoid copepods, amphipods, and an ostracod. The 0.4- to 0.6-mm size fraction was also taken; bivalve larvae, foraminifera, and cyclopoid copepods were found in many individuals. Other food items included the large cyclopoid copepod *Sapphirina*, a larval decapod, and masses of an unidentified greenish, fibrous material.

Sergia gardineri (Kemp 1913)

Vertical Distribution (Figure 21)

Sergia gardineri was usually found between 650 and 775 m during the daytime, although shrimp smaller than 5 mm CL seldom occurred below 700 m. The extremely high values in this range were largely due to the catches of the November 1972 cruise. On certain occasions the population seemed to extend downward to at least 1,200 m. The June 1973 cruise took 59 specimens in three tows between 850 and 1,050 m, and only 8 specimens in four tows between 650 and 850 m. The December 1970 cruise caught only nine specimens in an open tow at 650-680 m, but tows below 800 m caught large numbers, including 77 in a tow from 1,150 to 1,250 m. On the other hand, all four daytime tows on the May 1972 cruise between 650 and 950 m took only one shrimp.

The nighttime distribution was strongly influenced by large catches from the May 1973 cruise. It showed a concentration in the upper 150 m, with shrimp less than 6 mm CL restricted to 25-100 m. All large shrimp in the upper 25 m were females, the result of a single tow in May 1973 that fished between 15 and 45 m, taking 36 adult females and 1 very small male. A tow at 20 m on the same cruise took no *S. gardineri*, indicating that this species probably does not reach the surface. There were a few captures below the normal range on moonless nights, notably a 250-m tow in September 1971 that took four, and a 480- to 550-m tow in November 1972 that took five.

Most captures of *S. gardineri* on nights with much moonlight were at the daytime depth, except for the March 1971 cruise, which took 16 shrimp at 320-340 m and 20 shrimp at 100-150 m, although a tow at 170-200 m did not take any. Three open tows near full moon on the December 1970 cruise took 207 *S. gardineri* between 700 and 1,000 m, while a 550- to 600-m tow took 9. Later in the cruise when the moon was waning, they were captured at 80 and 30 m (but not at 100-110 or 50 m!). The

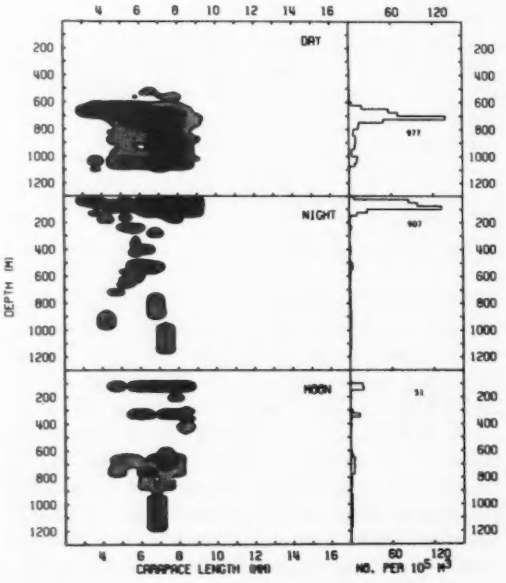

FIGURE 21.–Vertical distribution of *Sergia gardineri*.

December 1973 cruise took only two immature specimens at night in 10 oblique tows less than 650-m maximum depth. Six oblique tows from 400 to 1,200 m took a total of 62 shrimp, although high seas resulted in some catch spillage in two cases. *Sergia gardineri* clearly does not migrate near full moon.

Population Size, Growth, and Reproduction (Figure 22)

Sergia gardineri was by far the most numerous sergestid in the Teuthis collections, the average population density of 8.65 per 100 m^2 estimated from all horizontal tows being more than twice as high as the next most abundant species. Horizontal tows taking more than 100 shrimp occurred in February 1971 (night), June 1971 (day and night), November 1972 (day), and May 1973 (night). In addition, the open tows of the December 1970 cruise took large numbers, including 129 in a night tow. *Sergia gardineri* appeared to have been much less abundant during the first half of 1972, although most of these cruises occurred near full moon, when the normal vertical distribution patterns seem to be disrupted. The estimate from night tows affected by moonlight, 2.66 per 100 m^2, was much lower than the daytime or moonless night estimates. The oblique series of September 1972 and May 1973 gave figures of 10.00 and 1.90 per 100 m^2, respectively.

Recruitment was highest during the third quarter (July-September), although small shrimp began to enter the population in June. The median carapace length increased from 4.9 mm to 6.4 mm between the September 1972 and November 1972 cruises, giving a growth rate of about 1.2 mm CL per month. From November to May the growth rate was much lower, about 0.25 mm CL per month. The average size of females was largest in May, although a few very large females were still present in June. *Sergia gardineri* has a total life span of about 1 yr.

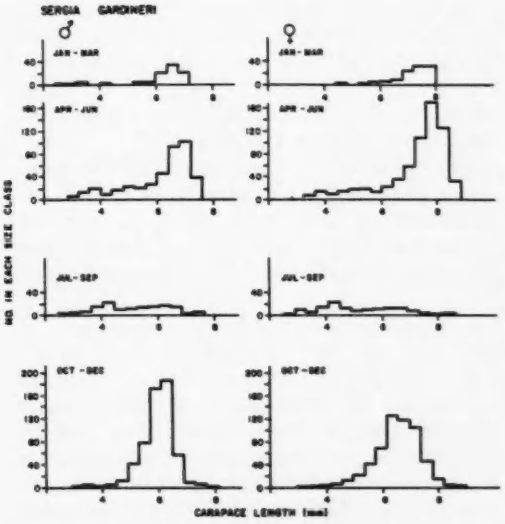

FIGURE 22.—Quarterly size-frequency distribution of *Sergia gardineri*.

Diet (Table 5)

Thirteen of the nineteen specimens of *S. gardineri* taken during DSB III had empty stomachs. The others contained calanoid copepods, an ostracod, a larval decapod, bivalve larvae, foraminifera, and greenish fibrous matter.

Sergia bigemmea (Burkenroad 1940)

Vertical Distribution (Figure 23)

Most of the few daytime captures of *S. bigemmea* during the Teuthis series were of immature shrimp less than 8 mm CL. A tow between 610 and 690 m took 15 in July 1971; 5 were caught in November 1972 in a tow probably around 750 m. The peak around 1,100 m resulted from two tows that fished as shallow as 820 m. Two of the three daytime captures of adults during the Teuthis series were between 1,000 and 1,100 m; the other was around 750-850 m. The December 1970 cruise took 20 adults in open tows between 800 and 1,200 m. The nighttime distribution varied with size; shrimp smaller than 10 mm CL generally occurred between 50 and 225 m, while the adults ranged between 125 and 250 m. The February 1973 cruise (DSB III) took several large hauls of *S. bigemmea*, including 49 specimens in a 1-h tow at 150-175 m. Only a few were caught under moonlit conditions; most of these were between 250 and 350 m. The December 1970 cruise took 5 *S. bigemmea* at 250 m and 11 at 750 m, indicating that much of the population was not migrating.

The vertical distribution patterns of *S. bigemmea* appeared to be affected by avoidance. While the females of most sergestid species grow considerably larger than the males, in *S. bigemmea*

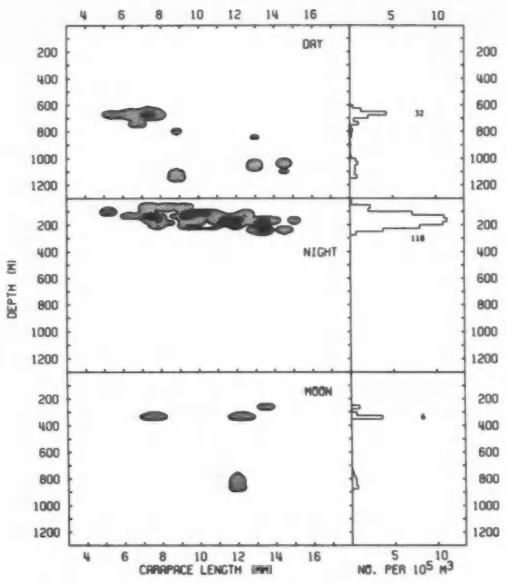

FIGURE 23.–Vertical distribution of *Sergia bigemmea*.

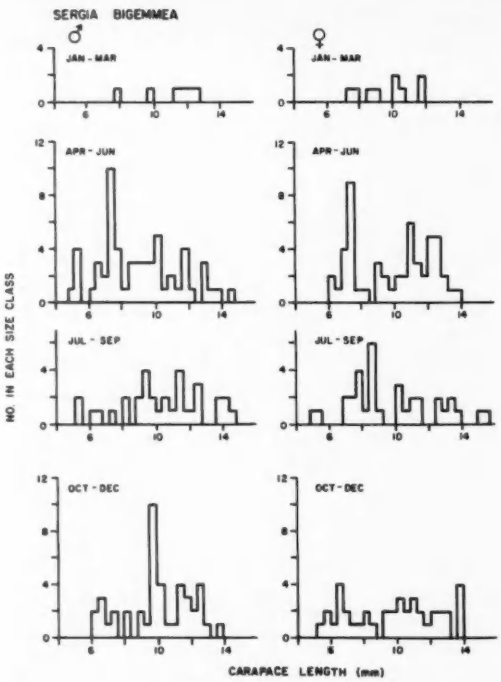

FIGURE 24.–Quarterly size-frequency distribution of *Sergia bigemmea*.

the maximum size was the same in both sexes, suggesting that the largest shrimp were escaping capture. Daytime catches were much smaller than nighttime catches, indicating that avoidance was more effective during the day. However, the maximum size captured was the same during the daytime as at night. It is curious that neither *Sergestes erectus* nor *Sergia fulgens* showed any signs of avoidance, though those caught are larger than *S. bigemmea*; perhaps *S. bigemmea* is particularly fast for its size or better at sensing the approach of the trawl.

Population Size, Growth, and Reproduction (Figure 24)

Sergia bigemmea was one of the less common sergestids in our collection; the average population density estimated from all horizontal tows was only 0.64 per 100 m^2. Most catches occurred at night, the figure for nighttime tows being 1.48 per 100 m^2. Very few *S. bigemmea* were captured during the first half of 1972, when most sampling was done near full moon. The oblique series of September 1972 took moderate numbers, producing a population density figure of 2.35 per 100 m^2, higher than any other all-red sergestid except *S. gardineri*. It was also moderately abundant during the December 1970 cruise, which had the only large daytime catch: 23 in an 800- to 900-m open IKMT tow. The largest catches of *S. bigemmea* occurred during the February 1973 cruise (DSB III) when it was the most abundant species taken, with 49 in a 1-h open tow. The May 1973 oblique series took only a handful, giving a population density estimate of 0.31 per 100 m^2.

None of the seasonal size-frequency histograms are significantly different from the others (Kolmogorov-Smirnov test: $P > 0.05$). Females larger than 12 mm CL were proportionately most abundant in the third quarter (July-September).

Diet (Table 5)

The surprisingly large catch of *S. bigemmea* during DSB III produced a more detailed picture of its diet than for the other species. Only 11 of the 88 shrimp had empty stomachs. *Sergia bigemmea* ate crustacean zooplankton, including calanoid copepods, amphipods, and ostracods; ostracods appeared to be a more important prey item than in the other species. Smaller prey were also

eaten—larval bivalves, small cyclopoid copepods, and foraminifera commonly occurring in the diet. *Sergia bigemmea* was the only species in which chaetognath spines were found. Other food items included the large cyclopoid copepod *Sapphirina*, a single larval decapod, and unidentified fibrous matter.

Sergia inequalis (Burkenroad 1940)

Vertical Distribution (Figure 25)

As with *S. bigemmea*, *S. inequalis* may have avoided the trawl. The few daytime captures were nearly all below 750 m; the peak near 550 m resulted from a tow in June 1971 that dipped to 760 m. Maximum daytime depth appeared to be 1,100-1,200 m. The December 1970 cruise took *S. inequalis* in open tows between 800 and 1,250 m—seven in a 950- to 1,000-m tow and four in a 1,150- to 1,250-m tow. The nighttime distribution varied with size. Small shrimp less than 12 mm CL were found in the upper 100 m; larger shrimp occurred between 100 and 250 m. Moonlight did not significantly affect the adults; there were no captures of small shrimp under these conditions. The Teuthis series showed no evidence of full moon nonmigration, but the December 1970 cruise took five specimens at night between 550 and 800 m.

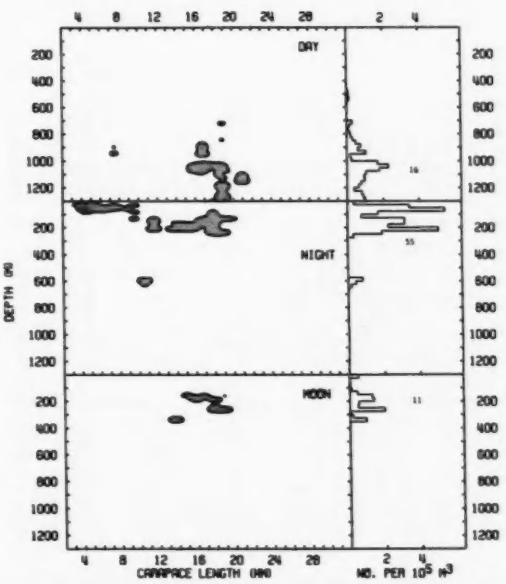

FIGURE 25.—Vertical distribution of *Sergia inequalis*.

Population Size, Growth, and Reproduction (Figure 26)

Sergia inequalis was not abundant in Hawaiian waters; the average population density estimated from all horizontal tows was only 0.55 per 100 m^2, less than any other regularly occurring all-red sergestid. The largest catch of adults was only seven, from an open tow in December 1970. The oblique series of September 1972 and May 1973 gave estimates of 0.94 and 0.31 per 100 m^2, respectively.

In spite of its relative rarity, *S. inequalis* showed a clear seasonal cycle of growth, although because of the small sample size, the differences among histograms are only marginally significant statistically (Kolmogorov-Smirnov test, II different from III, $0.10 > P > 0.05$). Recruitment was greatest in the second quarter (April-June), and

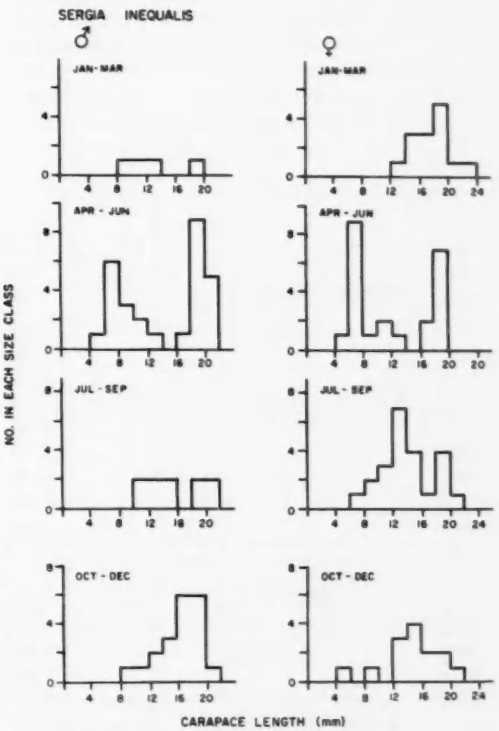

FIGURE 26.—Quarterly size-frequency distribution of *Sergia inequalis*.

the population increased in average size of individuals in succeeding quarters, the largest females being proportionately most abundant in the first quarter (January-March).

Diet (Table 5)

The single *S. inequalis* taken by DSB III had a calanoid copepod in its stomach.

Sergia bisulcata (Wood-Mason 1891)

Vertical Distribution (Figure 27)

As with *S. bigemmea*, equality in size of the sexes and small daytime catches indicate that *S. bisulcata* was avoiding the trawl. Immature shrimp were mostly taken between 675 and 750 m during the daytime, adults mostly from 700 to 900 m, with a few catches as deep as 1,100 m. The December 1970 cruise took 19 individuals, including both immatures and adults, in an open tow from 650 to 680 m, with much smaller catches down to 1,200 m. At night, immature shrimp occurred between 175 and 300 m, adults mostly from 225 to 350 m, with occasional captures as deep as 450 m. Moonlight depressed the population below 300 m; two tows at 450 m during the June 1973 cruise took 10 and 8 individuals, respectively. There was no evidence of full moon nonmigration.

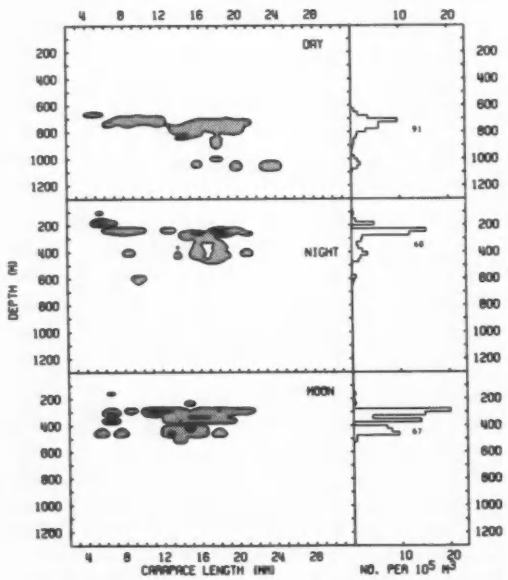

FIGURE 27.–Vertical distribution of *Sergia bisulcata*.

Population Size, Growth, and Reproduction (Figure 28)

Sergia bisulcata was the second most abundant all-red sergestid in the Teuthis collection, though far below *S. gardineri* in numbers. The average population density figure from all horizontal tows was 1.35 per 100 m^2. The figure for tows on moonlit nights was higher, 1.96 per 100 m^2, probably a sampling artifact. The two oblique series produced similar numbers; September 1972 gave 1.19 and May 1973 gave 0.82 per 100 m^2.

While quarterly variations in the size-frequency distributions of most Hawaiian sergestids suggest that they live about 1 yr, only in *S. bisulcata* is there evidence for a longer life span. Small immature shrimp around 7-9 mm CL were recruited in the second quarter (April-June) and grew to sexual maturity at about 14-18 mm CL in 1 yr. They continued to grow at a rate of approximately

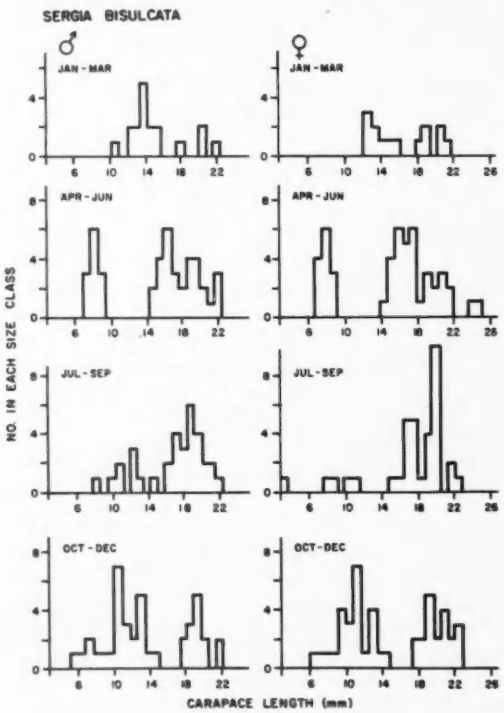

FIGURE 28.–Quarterly size-frequency distribution of *Sergia bisulcata*.

0.6 mm CL per month for up to one additional year. Few males appeared to live beyond 18 mo, but a few large females greater than 22 mm CL were probably a full 2 yr old. The pattern of growth appears clear cut, but the small sample size means that the data should be treated cautiously. The Kolmogorov-Smirnov test showed that only the third and fourth quarter size-frequency curves for the females were significantly different from each other ($0.05 > P > 0.01$).

Diet (Table 5)

Seven of the eight *S. bisulcata* taken by DSB III had food in their stomachs. Food items included ostracods, an amphipod, foraminifera, bivalve larva, and crustacean remains probably including a euphausiid and a larval decapod. No copepods were found, probably because of the small sample size.

Sergia maxima (Burkenroad 1940)

Only two individuals of this species were captured, one on the March 1972 cruise in a 480- to 615-m daytime tow and the other on the December 1973 cruise in an open tow between 400 and 550 m. Both individuals were immature males.

Sergia tenuiremis (Kröyer 1855)

Vertical Distribution (Figure 29)

During the daytime most of the population was below 800 m, although shrimp were sometimes taken as shallow as 700-750 m. A single immature individual was taken in June 1971 between 610 and 690 m. The deepest capture was in a tow between 1,220 and 1,500 m in August 1972. Tows below 1,500 m did not capture *S. tenuiremis*, but total trawling time in this region was rather small. Immature shrimp less than 15 mm CL were vertical migrators, moving up to 300-500 m at night. The adult population did not migrate as a whole, but part spread upward at night as shallow at 550-600 m. Moonlight had no effect on the nighttime vertical distribution of *S. tenuiremis*.

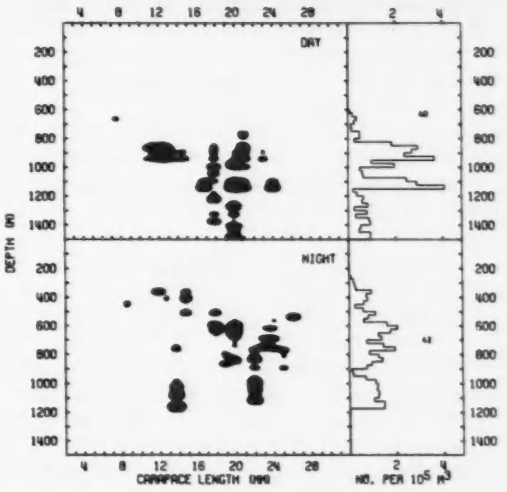

FIGURE 29.–Vertical distribution of *Sergia tenuiremis*. NIGHT and MOON data combined.

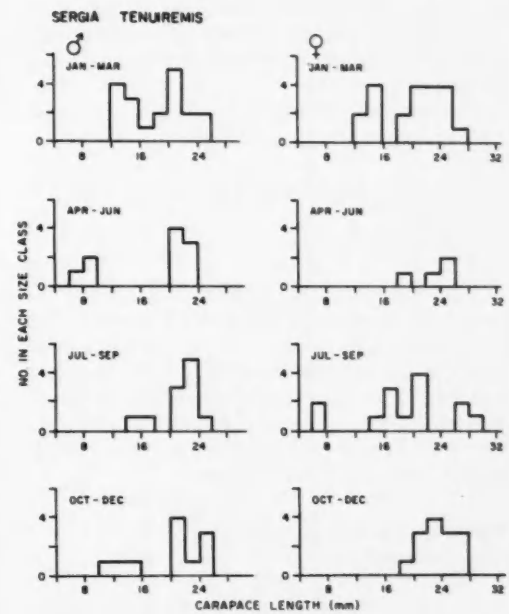

FIGURE 30.–Quarterly size-frequency distribution of *Sergia tenuiremis*.

Population Size, Growth, and Reproduction (Figure 30)

Sergia tenuiremis is not abundant in Hawaiian waters. The average population density estimated by all horizontal tows was 0.89 per 100 m², day and night values being similar. The two oblique series produced slightly smaller values, 0.67 per 100 m² in September 1972 and 0.70 in May 1973. Since these

series sampled only to 1,200 m, they may have missed the deeper portion of the population.

The seasonal size-frequency histograms are not significantly different from one another.

Diet (Table 5)

DSB III took only three specimens, all with empty stomachs.

Sergia laminata (Burkenroad 1940)

Vertical Distribution

Only four individuals were captured in closing tows, all in daytime tows during the November 1972 cruise. A tow at 650-725 m took three shrimp, and a tow at about 750-800 m took one shrimp. At night oblique tows in the upper 400 m took single shrimp during the September 1972 and May 1973 cruises, suggesting that *S. laminata* may be a vertical migrator. On the other hand, the December 1970 cruise captured one shrimp in an open horizontal tow at 550-600 m at night, suggesting that *S. laminata* may not migrate near full moon.

The small sample size did not allow studies of growth, reproduction, or diet.

Petalidium suspiriosum Burkenroad 1937

Vertical Distribution (Figure 31)

A deep-living nonmigrator, *P. suspiriosum* generally stayed below 800 m day and night. The shallowest captures came during the June 1972 cruise, which took six in a 750- to 800-m day tow and five in two night tows between 630 and 720 m. Maximum depth appeared to be at least 1,500 m; as with *S. tenuiremis*, limited trawling below 1,500 m did not catch any *P. suspiriosum*.

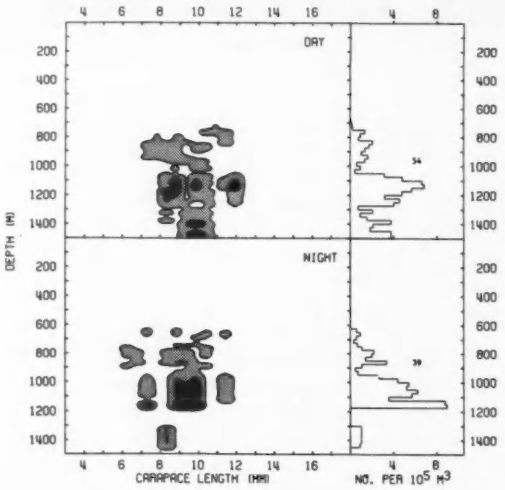

FIGURE 31.—Vertical distribution of *Petalidium suspiriosum*. NIGHT and MOON data combined.

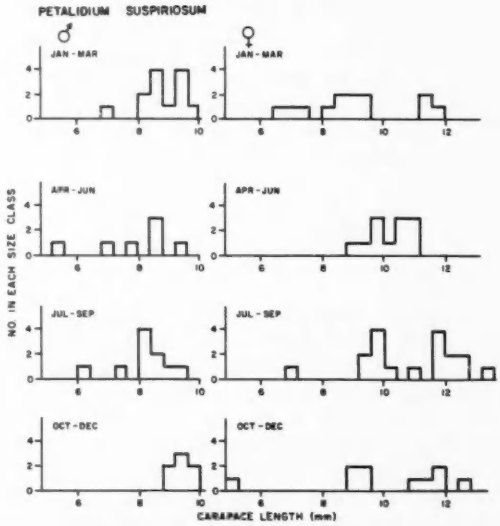

FIGURE 32.—Quarterly size-frequency distribution of *Petalidium suspiriosum*.

Population Size, Growth, and Reproduction (Figure 32)

Petalidium suspiriosum is more abundant than its small numbers in our collection would seem to indicate, since the depths below 800 m where it lives were not as thoroughly sampled as the shallower waters. The average population density estimated from all horizontal tows was 1.84 per 100 m^2, making it the second most abundant all-red sergestid. Like *S. tenuiremis*, the oblique series gave lower numbers, 1.21 per 100 m^2 in September 1972 and 1.31 in May 1973, probably because some of the population was below the 1,200 m maximum of the oblique tows.

Because of its susceptibility to damage, it was possible to make accurate measurements of carapace length on only about two-thirds of the specimens in the collection. There was no

significant seasonal trend in the size-frequency distributions of *P. suspiriosum*.

DSB III did not take *P. suspiriosum*, so its diet was not examined.

DISCUSSION

Color Pattern and Daytime Vertical Distribution: Role of Countershading

Sergestids display two basic color patterns. One group, including *Sergestes* and species of *Sergia* in Yaldwyn's (1957) "*S. challengeri*" species group, is "half-red," that is, its members are semitransparent except for the eyes and viscera, with red, stellate, subcuticular chromatophores scattered over the body and appendages, most concentrated on the cephalothorax. All half-red sergestids have well-developed photophores; *Sergestes* species have internal photophores, the organs of Pesta, and the half-red *Sergia* species have external cuticular lensed photophores. The other group, including the remaining species of *Sergia* and *Petalidium*, is "all-red," that is, its members are covered with a relatively uniform red cuticular pigment. All-red sergestids have simple lensless cuticular photophores or else lack photophores altogether.

Foxton (1970) showed that most mid-water decapods in the Fuerteventura area (Canary Islands) are either half-red or all-red. He found that half-red shrimps generally live shallower than 700 m during the daytime, while all-red shrimps generally live below 700 m. He concluded that the half-red color pattern and complex photophores are adaptations for concealment by countershading to match the light intensity of the surrounding waters when viewed from any angle, the photophores producing a ventrally directed beam of light to fill in the shadow of the animal. He suggested that the half-red pattern gives way to the all-red pattern at the depth where bioluminescent light becomes more important than penetrating surface light. Although many all-red decapods have simple photophores, he concluded that their function does not involve daytime countershading. Donaldson (1975) did not discuss this phenomenon, but an examination of his vertical distribution data for the Bermuda area shows the same daytime pattern of shallower half-red sergestids and deeper all-red sergestids, the dividing line again being approximately 700 m.

Other mid-water animals show similar depth-related changes in color patterns during the daytime. Badcock (1970) noted that mesopelagic fishes in the Fuerteventura area tend to be silvery above 650-700 m and dark below that depth. Amesbury (1975) found the same pattern in Hawaiian mesopelagic fishes, several independent analyses of community structure locating a major faunal boundary at 675-700 m between mostly silvery shallow mesopelagic fishes and mostly dark deep mesopelagic fishes.

Figure 33 shows how half-red and all-red sergestids differ in depth during the daytime in Hawaiian waters. The half-red species range from 425 to 725 m, with maximum abundance in the 600- to 625-m interval. The all-red species range from 625 to 1,500 m, with maximum abundance at 700-725 m.

Rather surprisingly, the depths of maximum abundance for the two types are only 100 m apart, and there is a large amount of overlap in their ranges, particularly in the zone between 650 and 725 m. Nearly half of the half-red sergestids below 650 m are *Sergestes erectus*, a species often taken in large numbers in tows that also take large

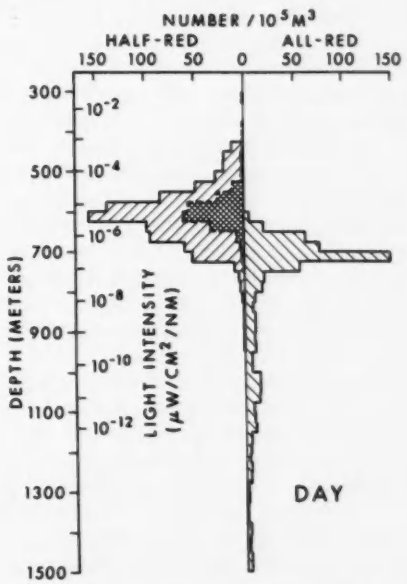

FIGURE 33.—Daytime vertical distribution of half-red and all-red Hawaiian sergestids. Half-red species are on the left (half-red *Sergia* spp. crosshatched), all-red species on the right. Scale of light intensity is from unpublished data of E. M. Kampa, at lat. 28°N.

numbers of *Sergia gardineri*, the most abundant all-red sergestid. To see if this overlap is real and not an artifact produced by vertical excursions of the trawl or seasonal variations in the position of a sharper transition depth, Teuthis XIX extensively sampled the 600- to 800-m zone in November 1972, using depth telemtery to try and maintain the trawl within a 25- to 50-m depth range. One tow between 630 and 680 m took 139 *Sergestes erectus* and 31 *Sergia gardineri*, another from 650 to 730 m took 157 *Sergestes erectus* and 289 *Sergia gardineri*, and a third from 700 to 740 m took 19 *Sergestes erectus* and 312 *Sergia gardineri*. On this occasion, at least, substantial numbers of both color patterns were living between 650 and 725 m.

Other investigators have found similar transition zones. In Hawaii, Riggs (pers. commun.) has found that the all-red species *Gennadas propinquus* (Penaeidae, Benthesicymae) lives as shallow as 600 m, with maximum numbers at 650-675 m. Ziemann (1975) obtained similar results for another all-red shrimp, *Systellaspis debilis* (Caridea, Oplophoridae), 75% of the adult population being found above 650 m on one occasion. In the Atlantic, Foxton's (1970) data show the half-red *Sergestes corniculum* (closely related to *S. erectus*) extending to at least 800 m, overlapping the ranges of the all-red species *Sergia robusta* and *Systellaspis debilis* (although most of the catch of the latter species were lighly pigmented juveniles). Donaldson's (1975) data show a transition zone from 650 to 800 m occupied by the half-red *Sergestes atlanticus* and *S. corniculum* and the all-red *Sergia grandis*. In view of this extensive overlap in the distribution of half-red and all-red decapods, it is necessary to review the conditions under which countershading is an effective concealment strategy and, in particular, Foxton's conclusion that only half-red decapods countershade.

The angular distribution of light in the mesopelagic environment is independent of solar elevation and depth (Denton and Nicol 1965). At any given point, the background light intensity is highest directly overhead, falling off rapidly to the sides, with a very low light intensity of backscattered light from below. The intensity of the background light 90° from the vertical is only 3-4% of the zenith value, decreasing to 0.3-0.5% at 180° from the zenith (Tyler and Preisendorfer 1962). Changes in surface irradiance or depth change the intensity but not its angular distribution. Countershading mechanisms match the animal to this background pattern; thus mid-water fishes use a dark dorsal surface, silvery sides, and ventral photophores for countershading (W. D. Clarke 1963; Nicol 1967; Badcock 1970). Foxton (1970) concluded that the half-red coloration of shallow mesopelagic decapods is a countershading mechanism using transparency rather than reflectors for lateral countershading. I propose that some deep mesopelagic all-red decapods also countershade ventrally and that ventral countershading can be effective below the transition zone from half-red to all-red decapods.

As depth increases and the intensity of the penetrating light dwindles, bioluminescence becomes relatively more and more important as a source of light in the mesopelagic environment. Bioluminescent light has a much different temporal and spatial distribution from the penetrating surface light. The bioluminescent light field is the sum of glows and flashes from many point sources whose angular distribution is more or less random. Countershading is an ineffective concealment strategy against bioluminescence; the silvery sides which camouflage a mid-water fish against the penetrating sunlight may in deeper water reflect a bioluminescent flash and reveal the fish against a black background. The best strategy of concealment in an environment lit only by random flashes is to be as nonreflective as possible. The dark brown or black fishes and all-red crustacea of the deep mesopelagic zone reflect blue light poorly (Nicol 1958), presumably indicating their use of this strategy.

Another effect of increasing depth is that the penetrating light eventually becomes too dim to be seen. The absolute visual threshold for deepsea fishes has been estimated as about 3×10^{-20} $\mu W / cm^2$ by Clarke and Denton (1962), a figure that undoubtedly varies in other groups of animals correlated with the degree of development of the eye. A slightly higher intensity is required before countershading becomes necessary. The maximum depth of effective countershading depends on the angular distribution of the penetrating light; thus in Hawaiian waters the threshold of lateral countershading is reached 110-120 m higher in the water column than the threshold for ventral countershading. Between these two depths lateral countershading is not needed but ventral countershading can still be effective.

The all-red sergestids with photophores appear to combine an antibioluminescent color pattern

with a ventral array of simple photophores for low-intensity ventral countershading. This interpretation implies that the transition from half-red to all-red sergestids at 650-725 m marks the upper limit of bioluminescence as an important source of ambient light. The lower limit of all-red sergestids with photophores should then mark the threshold of ventral countershading. Unfortunately, this study produced good daytime vertical distribution data for only one such species, *Sergia gardineri*. If its lower limit under normal conditions is typical of the other species, then the threshold of ventral countershading should lie at approximately 775 m. This depth is also the approximate upper limit of the two sergestids, *Sergia tenuiremis* and *Petalidium suspiriosum*, that lack photophores (Figures 29, 31). If 775 m is the threshold of ventral countershading, then the threshold for lateral countershading should be 110-120 m higher or about 660 m, approximately the depth of the transition from half-red to all-red sergestids.

It thus appears that the transition from half-red to all-red sergestids does not mark the absolute lower limit of countershading, but is related to the depth at which lateral countershading becomes ineffective and bioluminescent light forces a change in concealment strategy. Although the all-red color pattern hides the shrimp from bioluminescent flashes, enough of the penetrating light remains directly overhead that ventral countershading continues to be effective more than 100 m below the transition zone. The simple lensless photophores of the all-red sergestids presumably produce low levels of light in this dimly lit region. Other mid-water animals that lack lateral countershading mechanisms but have ventral arrays of photophores, such as many of the black stomiatoid fishes, may have evolved the same kind of camouflage.

Nighttime Vertical Distribution and Migration

The structure of the sergestid assemblage changes drastically as day gives way to night. All Hawaiian sergestid species except *Sergia tenuiremis* and *Petalidium suspiriosum* migrate into the upper 300 m of the water column. As figure 34 shows, the division into a shallow half-red and a deep all-red mesopelagic sergestid assemblage disappears on moonless nights. The species fall with little overlap into a shallow and a deep migratory group, adults of the shallow group

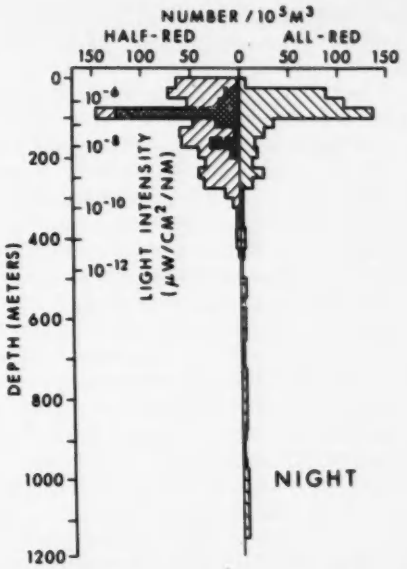

FIGURE 34.—Nighttime vertical distribution of half-red and all-red Hawaiian sergestids (moonless conditions). Hachure, etc., as in Figure 33. Light intensity estimated from unpublished daytime data of E. M. Kampa at lat. 28°N, using G. L. Clarke's (1968) values for relative intensity of day vs. night.

living in the upper 100 m, adults of the deep group living from 125 to 300 m. The shallow group includes *Sergestes vigilax*, *S. consobrinus*, *Sergia scintillans*, and *S. gardineri*. The deep group includes *Sergestes erectus*, *S. armatus*, *S. sargassi*, *Sergia bigemmea*, *S. inequalis*, and *S. bisulcata*. The single large nighttime capture of adult *Sergia fulgens* is at about 175 m, probably placing this species also in the deep group. In addition, *Sergestes pectinatus* is broadly distributed from 25 to 250 m, and *S. atlanticus* may likewise be broadly distributed if the single large catch in the upper 25 m is not representative of its normal distribution. T. A. Clarke (1973) found a similar pattern in the nighttime distribution of Hawaiian myctophid fishes, with a shallow group down to 125 m, a deep group at 150-250 m, and a few species broadly distributed in the upper 250 m. Closely related pairs of myctophid species separate into a shallow species and a deep species. Most sergestid species pairs are found at the same nighttime depths, except for *Sergestes armatus* and *S. vigilax*, and probably *Sergia scintillans* and *S. fulgens*.

The division of the nighttime sergestid assemblage at 100-125 m may possibly be related to

the penetrating surface light. The scale at the left of Figure 34 is an estimate, derived by assuming the value of light intensity at the surface on a moonless night to be 10^7 times fainter than during the day, a figure used by G. L. Clarke (1968), and applying this correction to the daytime light curve of E. M. Kampa (unpubl. data) used in Figure 33. The lower limit of daytime ventral countershading, estimated above as approximately 775 m, is equivalent to a nighttime depth of approximately 125-150 m, suggesting that the shallow group, but not the deep group may countershade at night. The lower limit of daytime lateral countershading, estimated as about 660 m, is equivalent to about 50 m at night, the approximate upper limit of *S. gardineri*, the shallowest all-red sergestid at night. Although these figures admittedly pile estimate on estimate, they suggest that light may influence the vertical distribution of sergestids at night as well as during the daytime.

W. D. Clarke (in Barham 1970:118) and Foxton (1970) have suggested that countershading may occur primarily at night in some mid-water animals. While nighttime ventral countershading appears feasible for some species of Hawaiian sergestids, these species all may need to countershade during the daytime also (Table 7). A number of species maintain approximately constant illumination day and night. Some species live in much brighter waters during the daytime than at night. No species, however, lives in brighter waters at night than during the daytime, as would be expected if countershading were occurring only at night.

Only two species of Hawaiian sergestids definitely do not migrate. *Sergia tenuiremis* appears to migrate to 300-400 m when less than 15 mm CL. The adult population spreads upward from an upper limit of 750-800 m during the day to about 600 m at night, although many shrimp remain in the daytime depth range. *Petalidium suspiriosum* remains below 750-800 m both day and night. Few Hawaiian sergestids occupy the depths between 300 and 600 m at night, in contrast to the Atlantic, where Donaldson (1973) found *Sergestes corniculum* and *Sergia grandis* and Foxton (1970) found *Sergestes corniculum* and *Sergia robusta* in this depth range. The reasons for this difference are unknown.

TABLE 7.—Estimated light intensities for daytime and dark night habitats of Hawaiian sergestids. Numbers are negative logarithms of light intensity (smaller numbers mean brighter light).

Species	Daytime habitat	Night habitat	
Sergestes atlanticus	5.0- 6.7	5.5- 6.0	D ~ N
Sergestes erectus	5.5- 6.7	9.0-10.0	D >>N
Sergestes armatus	4.7- 6.0	8.2- 9.7	D >>N
Sergestes vigilax	5.0- 6.7	5.5- 7.7	D ~ N
Sergestes orientalis	4.0- 5.2	5.5- 7.2	D > N
Sergestes consobrinus	4.7- 5.2	5.5- 6.2	D > N
Sergestes sargassi	3.5- 5.0	7.7- 9.5	D >>N
Sergestes pectinatus	4.2- 6.2	7.5- 9.0	D > N
Sergia fulgens	4.7- 5.5 ?	7.7- 8.2 ?	D > N ?
Sergia scintillans	4.2- 6.5	5.7- 7.2	D ~ N
Sergia gardineri	4.7- 7.2	5.7- 7.2	D ~ N
Sergia bigemmea	(7.0-11.0)	7.7- 9.0	D ~ N
Sergia inequalis	(7.0-11.0)	7.7- 9.0	D ~ N
Sergia bisulcata	6.5- 8.7	8.7-10.2	D > N

Although considerable evidence links diurnal vertical migration to the diurnal light cycle (e.g., Marshall 1954), the exact relation of light to vertical migration is complex and poorly understood. The simplest scheme, merely maintaining a constant light intensity around the clock, is not used by all Hawaiian sergestids, as Table 7 shows. The daytime sergestid assemblage cannot shift en masse to equivalent light levels at night, because the light intensity at the surface on a moonless night is approximately equivalent to that at 600 m during the daytime. Instead, we find species with similar daytime ranges but different nighttime ranges, such as *Sergestes armatus* and *S. consobrinus*; species with similar nighttime ranges but different daytime ranges, such as *Sergia scintillans* and *S. gardineri*; and species that exchange relative positions, such as *Sergestes sargassi* and *Sergia gardineri*. Vertical migration is a more complicated behavior than merely maintaining a constant light level.

A further complication of the vertical migration mechanism involves the response of sergestids to moonlight. When the moon increases the nighttime surface irradiance, the two groups of migrators react in different ways. The deep group remains relatively unaffected by moonlight, the young often moving downward to the depth of the adults. Moonlight drastically affects the shallow group, depressing most of the species below 150 m. The two assemblages, which separate by depth on dark nights, mix together on moonlit nights.

In addition to the normal response of sergestids to moonlight, there appears to be a period of about a week around full moon when some species stop migrating entirely, remaining at their daytime depths. This behavior is poorly shown by the results of the Teuthis cruises, showing up better in the supplementary data from 70-12 and Echo IV. Not all species react the same way to the full moon period. *Sergia gardineri* and probably *Sergestes*

atlanticus appear to stop migrating altogether. During cruise 70-12 part of the populations of *Sergestes orientalis* and *S. consobrinus* migrated, while the rest of the populations remained at their daytime ranges; during Echo IV both species appeared to migrate normally. Other species, such as *Sergestes vigilax* and *Sergia scintillans*, have shown no indications of nonmigratory behavior. Species showing the best evidence of nonmigration are all members of the shallow migratory group, but sampling was inadequate to determine definitely whether any species in the deep group are also nonmigrators. The data from cruise 70-12 and the June 1973 Teuthis cruise further suggest that when a species is not migrating its daytime depth can also be abnormal. *Sergia gardineri*, normally found between 650 and 775 m during the daytime, was taken as deep as 1,200 m on these cruises, and *Sergestes atlanticus*, normally found between 600 and 725 m, was taken down to 800 m.

The nonmigration of some sergestids around full moon is a separate behavior from the moonlight depression below 150 m. Nonmigration is not a direct effect of increased light levels. During Echo IV the moon was often heavily obscured by cloud, yet the nonmigratory species remained deep. During Cruise 70-12, nonmigratory species remained deep until the next-to-last night, when normal migration resumed, although light intensity in the surface waters could not have been radically different than on the previous night. Nonmigratory behavior has been observed in December and June, suggesting that it occurs during most seasons of the year.

Studies of seasonal variation in vertical migration can be complicated by moon effects. For example, Donaldson (1973) found abnormally deep distributions day and night for *Sergia splendens* during a February 1972 cruise. He also cited data from the same cruise showing that sergestid numbers were strongly influenced by moonlight in the upper 100 m, both at the quarter and at full. Knowing only that the moon was in various phases during the February 1972 cruise, it is impossible to separate seasonal effects from moonlight effects for *S. splendens*. Other mid-water groups show nonmigratory behavior not tied to lunar phase. Riggs (pers. commun.) found that species of the penaeid shrimp *Gennadas* did not migrate during our November 1972 cruise, which sampled near new moon when sergestids appeared to be migrating normally, and concluded that a seasonal factor was involved. In summary, the depth structure of the mesopelagic community changes in a bewilderingly complex manner under the influence of ambient light, lunar phase, season, and probably other undiscovered effects.

Feeding Chronology and Diet

In studies of the diets of mesopelagic animals, the time of day when feeding takes place is as interesting a datum as the kinds of prey eaten. The most widely accepted theory of the function of vertical migration holds that mesopelagic animals move into the food-rich shallow water at night to feed in the dark and retreat into deeper water at sunrise to escape the efficient visual predators of the epipelagic zone (Marshall 1954). If this theory is correct, an examination of the feeding chronology of vertical migrators should reveal that the majority, at least, of feeding occurs at night.

Table 4 compares the stomach contents of day-caught with night-caught sergestids from the DSB III cruise of February 1973. The night samples as a whole had a lower percentage of empty stomachs, a greater amount of food in the stomachs, and a lesser degree of digestion than the day samples, indicating that most feeding occurred at night. Unfortunately, only two species were abundant both day and night. *Sergestes armatus* fed more at night than during the daytime, although most specimens had empty stomachs regardless of time of day. *Sergestes erectus* actually had a lower percentage of empty stomachs during the daytime than at night, but the night specimens on the average were fuller than the day specimens. Other studies of feeding chronology in sergestids, notably those of Omori (1969) on *Sergia lucens*, Judkins and Fleminger (1972) on *Sergestes similis*, and Foxton and Roe (1974) on a variety of Atlantic species, also indicated that most feeding occurs at night. However, the DSB III day samples contained a number of individuals with appreciable amounts of food in their stomachs, showing that a certain amount of feeding occurs during the daytime. Donaldson (1973) found that *Sergestes sargassi*, *S. pectinatus*, and *Sergia japonica* appeared to feed around the clock. The first two species also live in Hawaiian waters; unfortunately, they only occurred in the night samples of DSB III, so this study could not test his observations.

If Hawaiian sergestid species have specialized by dietary preference, they might be expected to exhibit specialized structures for catching prey.

One important systematic character, the third maxilliped, appears directly related to feeding. Many species of *Sergestes* have greatly enlarged third maxillipeds, armed with stout spines and varying in length and development among the different species. *Sergestes pectinatus* in particular has highly modified third maxillipeds, with a series of short, comblike setae between the longer spines. The division of Hawaiian sergestids into a long-maxilliped group and a short-maxilliped group would seem logically to indicate a difference in diet between the two groups.

The results of the DSB III study (Table 5) are rather unexpected. All the species captured fed largely on zooplankton-sized crustacea in the 1- to 3-mm size range, chiefly calanoid copepods, myodocopid ostracods, and hyperiid amphipods. Some species also ate smaller zooplankton in the 0.4- to 0.6-mm size range, chiefly larval bivalves, foraminifera, and cyclopoid copepods. Ability to utilize prey in the small size range appeared to depend not on the length of the third maxillipeds but on the degree of setation of the first three pairs of pereiopods and (when not enlarged) the third maxillipeds. Species feeding on small zooplankton all have long setae spaced about 0.3-0.4 mm apart. All well-sampled species in the short-maxilliped group except *Sergestes erectus* fed on the small zooplankton. Within the long-maxilliped group, there is a gradation in degree of setation of the pereiopods from *S. armatus*, which has very short, sparse setae, through the *S. orientalis* group, which have somewhat longer, more numerous, but still rather sparse setae, to *S. sargassi* and *S. pectinatus*, which have rather long setae spaced about 0.5-0.6 mm apart. Of this group only *S. armatus* was captured in quantity during DSB III; its diet definitely lacked small zooplankton. A few specimens of *S. sargassi* and *S. pectinatus* were captured; none contained small zooplankton, but with the small sample size their status remains in doubt.

The dietary specializations of Hawaiian sergestids thus appear more related to size than to type of prey. The variety of copepods, amphipods, and ostracods that compose the large zooplankton fraction all seem to be equally acceptable as prey. The various modifications of the third maxilliped may reflect specialized methods of capturing prey rather than a specialized diet. In particular, the diet of *S. pectinatus* lacks any distinctive characteristics which can be associated with its unusual maxillipeds. While large zooplankters are probably seized individually, the small zooplankton appear to be sieved from the water onto the long setae, spaced so as to retain zooplankton and pass water, a process akin to filter feeding.

The small zooplankton probably represent a supplementary rather than a primary resource for sergestids. Larval bivalves, as meroplankton, are unlikely to be abundant all year around (they were abundant in the zooplankton during the December 1973 cruise; I have not examined other zooplankton samples) and are unlikely to be abundant far from land. Many of the individuals containing small zooplankton also contain masses of an unidentified greenish, fibrous material. Judkins and Fleminger (1972) reported similar material in *Sergestes similis*, and Foxton and Roe (1974) reported similar material in a number of Atlantic species. If this material is detritus and not the digested remains of some unidentified organism, it would represent another resource available to sieving sergestids, potentially very important when small zooplankton is sparse. The inefficient-looking sieving mechanism of the Hawaiian sergestids are a reminder that none of these species feed solely, or even primarily, on the small zooplankton. Any modifications for increased sieving ability must not hamper the animal's ability to seize large zooplankton.

The results from DSB III are quite different from those reported by Donaldson (1975). He found a much larger proportion of large prey, such as euphausiids and fishes, and also many more chaetognaths. Part of the difference is due to his much larger sample, where infrequently eaten prey are more likely to turn up. Large sergestids captured in very small numbers during the DSB III cruise, particularly *Sergia bisulcata*, *S. inequalis*, and perhaps *S. tenuiremis*, are likely to eat larger prey than is reported here. However, some of the difference between Donaldson's results and the DSB III results may be due to a higher degree of feeding in the trawl during Donaldson's study. The abnormal conditions in the cod end of a mid-water trawl are apt to lead to abnormal feeding. Judkins and Fleminger found a much lower proportion of euphausiids in the stomachs of sergestids caught by albacore than in trawl-caught shrimp. They also found fish scales only in trawl-caught shrimp, an unlikely food item under natural conditions. These results emphasize the need for future feeding studies to take whatever steps are necessary to minimize or eliminate feeding in the trawl.

Reproduction and Growth

It is diffcult to determine when sergestids spawn. Copulation occurs long before spawning; female *Sergia gardineri* whose ovaries have not started to mature often bear spermatophores. Eggs are spawned directly into the water rather than being carried on the appendages as in the carideans. Some spawning probably occurs year around, as sexually mature females can be captured at any time of the year. In *Sergestes*, the anterior lobes of the ovary vary greatly in size, filling much of the carapace at maximum development. However, there is no correlation of ovary development with carapace length in adult females. One possible explanation is that a female may spawn several batches of eggs over a period of several months, the ovaries regressing in size between batches.

Recruitment to a catchable size can be determined from the quarterly size-frequency histograms. Omori (1969) found that *Sergia lucens* required about 2 mo from spawning to recruitment; assuming the time is similar for Hawaiian species, a maximum in recruitment implies a maximum in spawning about one quarter earlier. Most Hawaiian sergestids showed peak recruitment in either the second (April-June) or third (July-September) quarter. Species with maximum recruitment in the second quarter included *Sergestes armatus*, *S. sargassi*, *Sergia inequalis*, and *S. bisulcata*. Species with maximum recruitment in the third quarter included *Sergestes atlanticus*, *S. consobrinus*, *S. pectinatus*, *Sergia scintillans*, and *S. gardineri*. Some species showed no significant difference from one quarter to the next; these included *Sergestes orientalis*, *Sergia bigemmea*, and probably *S. tenuiremis* and *Petalidium suspiriosum*. *Sergestes vigilax* had somewhat higher recruitment in quarters two and three than during the rest of the year. *Sergestes erectus* showed no particular recruitment maximum, but intermediate-sized shrimp were most abundant in the fourth quarter. *Sergia fulgens* is a peculiar case, to be discussed later.

Size-frequency data indicate that most Hawaiian sergestids appear to live about 1 yr, in agreement with most other studies (Pearcy and Forss 1969; Omori 1969; Donaldson 1973). The size-frequency histograms of *Sergia bisculcata* indicate that this species has a 2-yr life span, though the conclusion is based on a small sample. Donaldson concluded that *S. robusta* may also live 2 yr. Genthe (1969) arrived at a 2-yr life span for *Sergestes similis* off California, though Pearcy and Forss found a 1-yr life span for the same species off Oregon. Genthe asserted that juveniles less than 5 mm CL are 9 to 11 mo old, which seems too old. His data support a 1-yr life span if a 2- to 3-mo larval development time is assumed. Probably only a few large all-red species live more than a single year.

Sergia fulgens differed from all other Hawaiian species by showing an extremely modal size-frequency distribution and varying drastically in abundance from one month to the next (Figure 18). This behavior can best be explained by assuming that *S. fulgens* is an expatriate species occasionally moving into Hawaiian waters from elsewhere. Adult females from the December 1970 cruise and the May 1973 cruise (Teuthis XXI) had small ovaries with eggs about 150 μm in diameter. Mature females of the closely related but smaller species *S. scintillans* had proportionately larger ovaries with eggs about 260 μm in diameter. Omari (1969) reported an average diameter of 255 μm for another closely related species, *S. lucens*. It thus appears that the large female *S. fulgens* are not ripe. While it is possible that female *S. fulgens* continue to grow to 18 or 20 mm CL before spawning and that ripe females have never been captured, it seems more likely that *S. fulgens* do not reproduce in Hawaiian waters and that the local population is carried in by currents from its normal breeding range. Unfortunately, the geographic range of *S. fulgens* is almost totally unknown; in addition, it is very similar or identical to *S. talismani* in the Atlantic. Influxes of *S. fulgens* did not coincide with captures of *Sergestes tantillus*, an equatorial species occasionally found in Hawaiian waters, but little more can be inferred about the source of the local population of *S. fulgens*.

Interspecific Relationships

The 20 species of Hawaiian sergestids exhibit a variety of specializations in morphology and habit that appear to minimize interspecific competition and allow them to coexist as a stable assemblage. Most obvious is the division into half-red and all-red species, related to shallow and deep daytime depth ranges and the different concealment strategies required. The all-red sergestids are subdivided by size and nighttime vertical distribution, as are the half-red sergestids, which are also further subdivided by photophore type and

length of third maxillipeds. Finally, nearly all species cooccur with at least one other species that is much more closely related than any of the other Hawaiian sergestids. Interspecific competition should be strongest between members of a species pair; the ways in which two closely related sergestids divide up the mid-water environment should suggest the kinds of competition that occur in the mid-water environment and how competition is minimized.

Table 8 shows some observed parameters of Hawaiian sergestids. The dendrogramlike pattern at the left is a subjective representation of the affinities among the species, based on morphological features. Some differences will be noted in the vertical distribution patterns of the species pairs; for example, *Sergestes vigilax* is more broadly distributed than *S. armatus* and tends to live shallower at night. However, most species pairs are commonly found together over much of their vertical ranges. The most striking difference among closely related species is adult size. In every case the most closely related species show little or no overlap in the adult size range. For example, *Sergia scintillans* appears nearly identical to *S. fulgens*, differing chiefly in the number of photophores on the antennal scale and exopod of the uropod. However, adult *S. scintillans* vary from 5.5 to 10.5 mm CL, while adult *S. fulgens* vary from 11 to 16.5 mm CL. The only exception to this rule, the species triplet *Sergestes orientalis-S. tantillus-S. consobrinus*, is a revealing case. *Sergestes orientalis* is well separated in size from *S. consobrinus*, the largest females of *S. consobrinus* overlapping only slightly with the smallest males of *S. orientalis*. However, *S. tantillus*, while somewhat smaller in average size than *S. orientalis*, still overlaps considerably in size with the larger species. In this case it turns out that *S. tantillus* is primarily an equatorial species (Judkins 1972), occurring only rarely in Hawaiian waters. MacArthur (1972) has shown on theoretical grounds that when three similar species differ in only one parameter, such as body size, the competition pressures are strongest on the middle species. One of the factors determining the northern limit of *S. tantillus* may be this competition from both a larger and a smaller species.

Specialization solely by adult size could still result in competition if adults of the small species cooccur with similar-sized juveniles of the large species. In this case, other specializations appear to become important. When the species have similar vertical ranges, the juveniles may live shallower than the adults. For example, adult *Sergia bigemmea* and adult *S. inequalis* both occur at about 150 to 225 m at night. Juvenile *S. inequalis* in the 10- to 13-mm CL range, the size of adult *S. bigemmea*, are mostly found between 50 and 150 m, so that similar-sized individuals of the two species seldom occur together.

Competition could occur if the large species lives somewhat deeper than the small species, so that juveniles of the large species live at about the

TABLE 8.—Characteristics of Hawaiian sergestid species. Dendrogram shows estimated phylogenetic affinities among species.

Species	Adult size (CL, mm)	Day depth (m)	Night depth (m)	Population size (no./100 m²)
Sergestes orientalis	5.5-10	500- 625	0- 125	1.32
Sergestes tantillus	5.5- 8	450- 650?	0- 100?	<0.10
Sergestes consobrinus	3.8- 6	450- 725	0- 75	1.05
Sergestes armatus	9 -14.5	550- 650	150- 300	2.35
Sergestes vigilax	6 - 8.5	550- 725	0- 200	0.35
Sergestes atlanticus	5 - 9	550- 725	0- 300	1.31
Sergestes cornutus	3.5- 5	450- 550?	(0- 50)?	<0.10
Sergestes erectus	13 -24.5	550- 800	250- 325	3.81
Sergestes sargassi	7 -10.5	450- 575	125- 300	0.70
Sergestes pectinatus	3.2- 7.5	450- 725	75- 275	1.71
Sergia fulgens	11 -16.5	550- 625?	75- 200?	2.26
Sergia scintillans	5.5-10.5	525- 700	25- 125	3.31
Sergia gardineri	4.5- 9	650- 775	25- 150	8.65
Sergia bigemmea	9.5-14.5	750-1,100?	125- 250	0.64
Sergia inequalis	13.5-22	750-1,100?	100- 250	0.55
Sergia bisulcata	16.5-23	700- 900	225- 350	1.35
Sergia maxima	(41.5)	?	?	<0.10
Sergia tenuiremis	18.5-29	750-1,300+	550-1,200+	0.89
Sergia laminata	7 -10	700- 800?	?	<0.10
Petalidium suspiriosum	8.5-12	800-1,300+	800-1,200+	1.84

same depth as adults of the small species. The clearest example of this type in Hawaiian waters is *Sergestes vigilax* and *S. armatus*, where most juvenile *S. armatus* in the 6- to 8.5-mm CL range live around 100 to 150 m at night, overlapping somewhat with adult *S. vigilax* in the same size range (most *S. vigilax* live above 100 m, but adults often occur somewhat deeper). However, it appears that adult *S. vigilax* are most abundant from October to March, while juvenile *S. armatus* in the same size range are most abundant from April to June (Figures 6, 8). Thus the actual overlap at any one time is probably small.

The Hawaiian sergestid assemblage can thus be described by size, morphology, and vertical distribution. Consider the half-red species first. Those with short maxillipeds are divided into a pair of species with lensed cuticular photophores and three species with organs of Pesta. The pair with cuticular photophores includes a large species, *Sergia fulgens*, and a small species, *S. scintillans*; these species may also live at different depths at night. Of the three species with organs of Pesta, *Sergestes erectus* is very large, distantly related to the other two, and lives deeper at night; *S. atlanticus* is larger than *S. cornutus* and may live deeper during the daytime. Long third maxillipeds appear to have evolved at least twice, possibly three times, in *Sergestes* (Burkenroad 1937; Foxton 1972). The *S. sargassi-S. pectinatus* pair is distinct from the others; again, *S. sargassi* is large and *S. pectinatus* is small, with specialized maxillipeds and broader vertical distributions day and night. The other two groups are more closely related, but the *S. armatus-S. vigilax* pair has longer maxillipeds than the *S. orientalis-S. tantillus-S. consobrinus* triad. *Sergestes armatus* is larger than *S. vigilax* and lives deeper at night; the other group has been discussed above.

Among the all-red Hawaiian sergestids, a similar organization prevails. The *Sergia inequalis-S. bigemmea-S. gardineri* group are respectively large, medium-sized, and small; in addition, *S. gardineri* lives shallower than the other two at night, and perhaps during the daytime. The *S. bisulcata-S. maxima* pair is related to the above triad, but *S. bisulcata* is somewhat larger than *S. inequalis* and lives deeper at night, while the rare *S. maxima* is extremely large. Two species without photophores are nonmigrators; *S. tenuiremis* is much larger than *Petalidium suspiriosum*. The rare *S. laminata*, while related to *S. tenuiremis*, is smaller, has photophores (Walters 1975), and appears to migrate.

Studies of sergestid assemblages in the subtropical Atlantic by Foxton (1970) near Fuerteventura (Canary Islands) and Donaldson (1975) near Bermuda showed interesting parallels to the present study in the subtropical Pacific (Table 9). The two Atlantic areas were very similar to one

TABLE 9.—Atlantic and Hawaiian sergestid assemblages.

Hawaii	Bermuda[1]	Fuerteventura[2]
Sergestes consobrinus	*(Sergestes edwardsii)*	n.e.[3]
Sergestes orientalis / *(Sergestes tantillus)*	n.e.	n.e.
Sergestes armatus	*Sergestes armatus*	*Sergestes armatus*
Sergestes vigilax	*Sergestes vigilax*	*Sergestes vigilax*
Sergestes atlanticus	*Sergestes atlanticus*	*(Sergestes atlanticus)*
(Sergestes cornutus)	*Sergestes cornutus*	n.e.
Sergestes erectus	*"Sergestes corniculum"*[4]	*"Sergestes corniculum"*[4]
Sergestes sargassi	*Sergestes sargassi*	*Sergestes sargassi*
Sergestes pectinatus	*Sergestes pectinatus*	*Sergestes pectinatus*
Sergia fulgens	*(Sergia talismani)*	n.e.
Sergia scintillans	n.e.	n.e.
Sergia gardineri / *Sergia bigemmea*	*Sergia splendens*	*Sergia splendens*
Serga inequalis	*Sergia robusta*	*Sergia robusta*
Sergia bisulcata / *Sergia maxima*	*Sergia grandis*	n.e.
(Sergia laminata)	*(Sergia filicta)*	n.e.
Sergia tenuiremis	*Sergia tenuiremis*	*Sergia tenuiremis*
n.e.	*Sergia japonica*	*Sergia japonica*
Petalidium suspiriosum	—	—

[1]From Donaldson (1975).
[2]From Foxton (1970).
[3]n.e. — no equivalent.
[4]See text.

another except for the abundance of *Sergestes atlanticus* and *Sergia grandis* (Sund 1920) in Bermuda relative to Fuerteventura (the Fuerteventura material all came from a single cruise and may have lacked some of the less-abundant species). More surprising, the Atlantic sergestids were very similar to the Hawaiian species, particularly the half-red types. "*Sergestes corniculum* Krøyer 1855"[3] replaced its close relative, *S. erectus* in the Atlantic, and two rare Bermuda species, *S. edwardsii* Krøyer 1855 and *Sergia talismani* (Barnard 1947), had close relatives, *Sergestes consobrinus* and *Sergia fulgens*, in Hawaiian waters; otherwise, all the half-red species in the two Atlantic studies also occurred in the present study. There were some differences in abundance and vertical distribution, partly real and partly due to differences in sampling. *Sergestes vigilax* was more abundant than *S. armatus* in the Atlantic studies, and *S. sargassi* was more abundant than *S. pectinatus*; the opposite was true in Hawaiian waters. *S. atlanticus* was more abundant near Bermuda and less abundant near Fuerteventura than near Hawaii. *Sergestes corniculum* was more broadly distributed at night than its Hawaiian counterpart, *S. erectus*. The biggest differences were the rarity or absence in the Atlantic collections of the *S. orientalis* types and the half-red *Sergia* species, both of which were abundant in Hawaiian waters. Still, the similarities between the subtropical Atlantic and Pacific were considerable: one or more large species with short third maxillipeds and with fairly deep nighttime distributions, one or two smaller species with short maxillipeds and living shallower at night (in Bermuda), and a variety of species with long maxillipeds occurring in closely related groups of large and small species.

The all-red sergestids also showed similarities between the subtropical Atlantic and Pacific, although the parallelism was not as striking as in the half-red types. *Sergia tenuiremis* was found in all three areas. The role of *S. gardineri* was filled in the Atlantic by the closely related *S. splendens* (Sund 1920). It was somewhat larger than *S. gardineri*, exceeding 11 mm CL, but had no potential competition in the 10- to 15-mm CL size range like the Hawaiian *S. bigemmea*. The nearest Atlantic equivalents of *S. inequalis* and *S. bisulcata*, respectively *S. robusta* (Smith 1882) and *S. grandis*, lived much deeper at night, in the 400- to 600-m zone, which was nearly devoid of sergestids around Hawaii. *Sergia filicta* (Burkenroad 1940) may be the Atlantic counterpart of *S. laminata*, but very little is known about either species. *Sergia japonica* (Bate 1881) had no Hawaiian equivalent, and *S. maxima* had no Atlantic equivalent. Neither Atlantic study mentioned *Petalidium*, so it is unclear whether there is an Atlantic counterpart to the Hawaiian *Petalidium suspiriosum* (*P. foliaceum* Bate 1881 occurs in the South Atlantic (Kensley 1971)). Both oceans thus contain an all-red assemblage consisting of one or more nonmigrators, a small, abundant species with a shallow nighttime range, and several larger species living deeper at night. In general, the Hawaiian area appears to have more half-red and fewer all-red sergestid species than the subtropical Atlantic.

While the parameters of Table 8 indicate that Hawaiian sergestids have partitioned the midwater environment, this study has left unclear the ecological significance of most of the parameters. Differences in size, length of third maxilliped, and nighttime vertical range are presumably related to diet, but the data on feeding show little dietary specialization other than the ability of some species to eat submillimeter-sized zooplankton. A more elaborate study may reveal more subtle variations in diet, perhaps related to vertical distribution of prey or differences in hunting strategies. Daytime vertical distribution and color pattern seem most likely related to predation. Virtually nothing is known about predation on Hawaiian sergestids. The division of half-red sergestids into species with organs of Pesta and species with lensed cuticular photophores has an unknown ecological significance. Cuticular photophores are fixed in position, but I have observed sergestids with organs of Pesta rotating them through nearly 180°, maintaining a vertical orientation of the photophores regardless of the attitude of the animal (see also Omori 1974). Studies of live sergestids may reveal differences in behavior between the two groups related to the need for ventral countershading. Hawaiian sergestids appear to occupy distinct niches, but the niches cannot be defined yet in an ecologically meaningful way.

[3]Crosnier and Forest (1973) have reviewed the systematics of Atlantic species of Yaldwin's "*Sergestes corniculum*" species group. They replaced *S. corniculum* Krøyer with *S. henseni* (Ortmann 1893) and three new species—*S. paraseminudus*, *S. pediformis*, and *S. curvatus*. Donaldson's figure of *S. corniculum* corresponded to *S. curvatus*. Foxton gave no drawings of *S. corniculum*, but a later study in the same area, Foxton and Roe (1974) found *S. henseni* and *S. curvatus*.

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LITERATURE CITED

AMESBURY, S. S.
1975. The vertical structure of the micronektonic fish community off leeward Oahu. Ph.D. Thesis, Univ. Hawaii, Honolulu, 176 p.

BADCOCK, J.
1970. The vertical distribution of mesopelagic fishes collected on the Sond Cruise. J. Mar. Biol. Assoc. U.K. 50:1001-1044.

BARHAM, E. G.
1957. The ecology of sonic scattering layers in the Monterey Bay area. Stanford Univ., Hopkins Mar. Stn. Tech. Rep. 1, 182 p.
1970. Deep-sea fishes: Lethargy and vertical orientation. *In* G. B. Farquar (editor), Proceedings of an International Symposium on Biological Sound Scattering in the Ocean, p. 100-118. Maury Cent. Ocean Sci. Rep. 005.

BURKENROAD, M. D.
1937. The Templeton Crocker Expedition. XII. Sergestidae (Crustacea Decapoda) from the Lower Californian region, with descriptions of two new species and some remarks on the organs of Pesta in *Sergestes*. Zoologica (N.Y.) 22:315-329.

CLARKE, G. L.
1968. Light measurements. BioScience 18:965-966.

CLARKE, G. L., AND E. J. DENTON.
1962. Light and animal life. *In* M. N. Hill (editor), The sea, Vol. 1, p. 456-468. Interscience, N.Y.

CLARKE, T. A.
1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 71:401-434.

CLARKE, W. D.
1963. Function of bioluminescence in mesopelagic organisms. Nature (Lond.) 198:1244-1246.

CROSNIER, A., AND J. FOREST.
1973. Les crevettes profondes de l'Atlantique oriental tropical. Faune Tropicale, Tome XIX. ORSTOM (Off. Rech. Sci. Tech. Outre-Mer), Paris, 409 p.

DENTON, E. J., AND J. A. C. NICOL.
1965. Reflexion of light by external surfaces of the herring, *Clupea harengus*. J. Mar. Biol. Assoc. U.K. 45:711-738.

DONALDSON, H. A.
1973. Ecology of the Genus *Sergestes* (Decapoda, Natantia) in an area near Bermuda. Ph.D. Thesis, Univ. Rhode Island.
1975. Vertical distribution and feeding of sergestid shrimps (Decapoda: Natantia) collected near Bermuda. Mar. Biol. (Berl.) 31:37-50.

DOTY, M. S., AND M. OGURI.
1956. The island mass effect. J. Cons. 22:33-37.

FOXTON, P.
1970. The vertical distribution of pelagic decapods (Crustacea: Natantia) collected on the Sond Cruise 1965. II. The Penaeidea and general discussion. J. Mar. Biol. Assoc. U.K. 50:961-1000.
1972. Further evidence of the taxonomic importance of the organs of Pesta in the genus *Sergestes* (Natantia, Penaeidea). Crustaceana 22:181-189.

FOXTON, P., AND H. S. J. ROE.
1974. Observations on the nocturnal feeding of some mesopelagic decapod crustacea. Mar. Biol. (Berl.) 28:37-49.

GENTHE, H. C., JR.
1969. The reproductive biology of *Sergestes similis* (Decapoda, Natantia). Mar. Biol. (Berl.) 2:203-217.

GILMARTIN, M., AND N. REVELANTE.
1974. The 'island mass' effect on the phytoplankton and primary production of the Hawaiian Islands. J. Exp. Mar. Biol. Ecol. 16:181-204.

GORDON, D. C., JR.
1970. Chemical and biological observations at station Gollum, an Oceanic Station near Hawaii, January 1969 to June 1970. Hawaii Inst. Geophys., Tech. Rep. HIG-70-22, 44 p.

GUNDERSON, K., C. W. MOUNTAIN, D. TAYLOR, R. OHYE, AND J. SHEN.
1972. Some chemical and microbiological observations in the Pacific Ocean off the Hawaiian Islands. Limnol. Oceanogr. 17:524-531.

JUDKINS, D. C.
1972. A revision of the decapod crustacean genus *Sergestes* (Natantia, Penaeidea) *sensu lato*, with emphasis on the systematics and geographical distribution of *Neosergestes*, new genus. Ph.D. Thesis, Univ. California, San Diego, 289 p.

JUDKINS, D. C., AND A. FLEMINGER.
1972. Comparison of foregut contents of *Sergestes similis* obtained from net collections and albacore stomachs. Fish. Bull., U.S. 70:217-223.

KENSLEY, B. F.
1971. The family Sergestidae in the waters around Southern Africa (Crustacea, Decapoda, Natantia). Ann. S.-Afr. Mus. 57:215-264.

MACARTHUR, R. H.
1972. Geographical ecology: Patterns in the distribution of species. Harper & Row, Publishers, Inc., N.Y., 269 p.

MARSHALL, N. B.
1954. Aspects of deep sea biology. Philosophical Library, N.Y., 380 p.

MAYNARD, S. D., F. V. RIGGS, AND J. F. WALTERS.
1975. Mesopelagic micronekton in Hawaiian waters: Faunal composition, standing stock, and diel vertical migration. Fish Bull., U.S. 73:726-736.

NAKAMURA, E. L.
1967. Abundance and distribution of zooplankton in Hawaiian waters 1955-56. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 544, 37 p.

NICOL, J. A. C.
1958. Observations on luminescence in pelagic animals. J. Mar. Biol. Assoc. U.K. 37:705-752.
1967. The luminescence of fishes. Symp. Zool. Soc. Lond. 19:27-55.

OMORI, M.
1969. The biology of a sergestid shrimp, *Sergestes lucens* Hansen. Univ. Tokyo, Bull. Ocean Res. Inst. 4, 83 p.
1974. The biology of pelagic shrimps in the ocean. Adv. Mar. Biol. 12:233-324.

OMORI, M., A. KAWAMURA, AND Y. AIZAWA.
1972. *Sergestes similis* Hansen, its distribution and importance as food of fin and sei whales in the North Pacific Ocean. *In* A. Takenouti (editor), Biological oceanography of the northern North Pacific Ocean, p. 373-391. Idemitsu Shoten, Tokyo.

PEARCY, W. G., AND C. A. FORSS.
1969. The oceanic shrimp *Sergestes similis* off the Oregon coast. Limnol. Oceanogr. 14:755-765.

TYLER, J. E., AND R. W. PREISENDORFER.
1962. Transmission of energy within the sea. *In* M. N. Hill (editor), The sea, Vol. 1, p. 397-451. Interscience, N.Y.

WALTERS, J. F.
1975. Ecology of Hawaiian sergestid shrimps (Penaeidea: Sergestidae). Ph.D. Thesis, Univ. Hawaii, 227 p.

YALDWYN, J. C.
1957. Deep-water crustacea of the genus *Sergestes* (Decapoda, Natantia) from Cook Strait, New Zealand. Zool. Publ., Victoria Univ., Wellington (N.Z.) 22:1-27.

ZIEMANN, D. A.
1975. Patterns of vertical distribution, vertical migration, and reproduction in the Hawaiian mesopelagic shrimp of the family Oplophoridae. Ph.D. Thesis, Univ. Hawaii, 112 p.

DECISION THEORY APPLIED TO THE SIMULATED DATA ACQUISITION AND MANAGEMENT OF A SALMON FISHERY[1]

GARY E. LORD[2]

ABSTRACT

A salmon fishery management model utilizing statistical decision theory has been constructed. The model provides for the successive acquisition of data that can be used to formulate and maintain an optimum management strategy. The Bayes risk is defined as the expected economic loss resulting from a set of fishery management decisions and the criterion of optimality is taken to be the strategy that minimizes the Bayes risk. Specific functional forms are assumed where necessary in order to obtain a closed form expression for the Bayes risk. The Bayes risk, in units of numbers of fish, can then be computed for any particular sequence of fishery management decisions.

This paper represents a continuation of an earlier effort (Lord 1973) in which statistical decision theory was applied to the data acquisition and management of a salmon fishery. The crucial feature was not that the species considered was salmon but that the assumed fishery was both dynamic and subject to errors in the population estimation. The population is assumed to be subject to continuing assessment, however, so that as the season progresses it is possible to make repeatedly more refined estimates of the true state of nature. The management strategy may thus be modified successively to reflect the additional data as they become available.

The development was quite abstract and presented only the basic theory in a relatively general way. The present paper represents an intermediate situation in which the theory is applied to a specific model constructed to represent such a fishery. The principal features of this model are: 1) a Ricker spawner-return relationship, 2) simulated sampling for population estimation purposes, and 3) an economic loss function based on maximum substained yield (MSY).

A limitation of the present model is that it is constructed in such a manner that a closed analytic form is obtained without recourse to Monte Carlo or other approximate methods of analysis. In other words, the Bayes risk may be computed exactly upon the specification of well defined sets of parameters. The imposition of such analytical requirements constrains the choice of functions to those that are mathematically tractable. Anticipating the final results, Equations (18) and (20), I feel that about the maximum degree of generality has been retained consistent with analytical tractability. It is likely that models possessing a greater degree of fidelity to the actual fishery situations will require the use of Monte Carlo methods as Mathews (1966) used in his simulation of the cannery portion of the Bristol Bay fishery.

ANALYSIS

The notation used in Lord (1973), with only minor changes, will be retained here. In this section I will discuss the Bayes risk for a particular fisheries model based on the Ricker spawner-return relation. The criterion of optimality will be taken as MSY. Economic losses will accrue as the actual management strategies depart from the optimum. Generally these losses will be reflected in either a decreased present catch or in diminished future returns due to prior overfishing.

A loss function proportional to the difference between the optimum catch and the actual catch, on an MSY basis, will be assumed. This is a simple and intuitively reasonable concept but, nonetheless, a unique formulation of the loss function from this criterion is no simple task. The difficulty arises from the use of a spawner-return relation which reflects the biological fact that the present state of the system is necessarily the result of past actions and, similarly, that future conditions will depend on present actions. In the case of sockeye salmon,

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an added complication is provided by the fact that the run in any year represents the progeny of several spawning groups.

The Ricker spawner-return relation, for a single spawning group, is given by

$$R_n = aE_{n-k}e^{-bE_{n-k}} \tag{1}$$

where R_n is the return in year n resulting from an escapement E_{n-k} k years prior, e is the base of natural logarithms, and a and b are parameters assumed unique for any river system or spawning group. We may generalize Equation (1) to the case of multiple spawning groups to give

$$R_n = \sum_{k=1}^{K} a_k E_{n-k} e^{-bE_{n-k}} \tag{2}$$

where the relevant spawning occurs over the years $(n-1)$ through $(n-K)$. In Equation (2) the coefficients (a_k) now reflect not only the magnitude of the run, as in Equation (1), but the proportion of the run arising from each spawning group. Specifically we can write $a_k = ap_k$ where a is the parameter in Equation (1) and p_k is proportion of the run in year n arising from spawners in year $(n-k)$. We have the condition $\sum_{k=1}^{K} p_k = 1$ from which it follows that $\sum_{k=1}^{K} a_k = a$.

The return as given by Equation (1) or Equation (2) is a deterministic function of the parameters. In actual practice, however, the return, from the biologist's point of view, is a random variable in which case some additive or multiplicative error term must be appended to Equation (1). Thus, at an appropriate point in the analysis, the return will be assumed to be a random variable whose expected value is given by Equation (1).

Let X_n be the catch in year n. Then

$$X_n = a\sum_{k=1}^{K} p_k E_{n-k} e^{-bE_{n-k}} - E_n .$$

Let X_{tot} be the total catch over some fixed but otherwise arbitrary number, say n^*, of fishing seasons. Then

$$X_{tot} = \sum_{n=1}^{n^*}\left[\sum_{k=1}^{K} a_k E_{n-k} e^{-bE_{n-k}} - E_n\right]. \tag{3}$$

If we attempt to maximize X_{tot} with respect to the yearly escapements $E_1, E_2, \ldots E_{n^*}$, it turns out that as $n^* \to \infty$: a) a steady state solution exists and b) the optimum steady state escapement, E_0, is that which maximizes the function $(aEe^{-bE} - E)$.

Let L_n denote the economic loss in any year n and define L_n as the difference between the optimum catch, X_{opt}, and the actual catch X_{act}, i.e., $L_n = X_{opt} - X_{act}$. From Equation (3) we obtain

$$L_n = (aE_0e^{-bE_0} - E_0) - \left(a\sum_{k=1}^{K} p_k E_{n-k} e^{-bE_{n-k}} - E_n\right). \tag{4}$$

E_0 is fixed and all of the escapements $(E_{n-k})(k = 1 \ldots K)$ have already occurred thus leaving only E_n at our disposal. L_n is clearly minimized by setting $E_n = 0$ but since this would eliminate a portion of the run in future years the subsequent loss would be high indeed. Consider now the combined loss for two successive years n and $(n+1)$. Proceeding along the same lines that led to Equation (4) we obtain

$$L_n + L_{n+1} = 2(aE_0e^{-bE_0} - E_0) - \left(a\sum_{k=1}^{K} p_k E_{n-k} e^{-bE_{n-k}} - E_n\right) - \left(a\sum_{k=1}^{K} p_k E_{n+1-k} e^{-bE_{n+1-k}} - E_{n+1}\right).$$

If this is treated as a function of the single variable E_n, an optimum value can be obtained. However, this loss also depends on E_{n+1} which has not yet occurred. Let us extend this process through year $(n+K)$, which is a convenient stopping point since it represents the completion of a cycle starting at year n. The total loss over this period is given by

$$L_{n,n+K} = (K+1)\left(aE_0e^{-bE_0} - E_0\right) - \sum_{j=n}^{n+K}\left[a\sum_{k=1}^{K} p_k E_{j-k} e^{-bE_{j-k}} - E_j\right]. \tag{5}$$

The loss given by Equation (5) depends not only on past and present escapements but on the future values $E_{n+1}, E_{n+2}, \ldots E_{n+K}$ as well. Thus, when formulating a policy for any particular year one must take into account future policies also. From a mathematical point of view what we have emerging here is another dynamic program, i.e., the optimum year-to-year allocation as well as the within-year allocation is in the form of a dynamic program. This is too great an anlytical burden to

bear. However, we can invoke the "Principle of Optimality" (Bellman 1957:83) to specify that $E_{n+j} = E_0$ for all $j \geq 1$, i.e., all future escapements are assumed to be the optimum MSY escapement. This is a reasonable assumption since the principle of optimality states that an optimal policy is one which, given the present state of the system, establishes and maintains an optimal policy for all future time periods. Since E_0 represents such an optimum steady state escapement it follows that $E_{n+j} = E_0$ for future optimality. In this case Equation (5) takes the form

$$L_{n,n+K} = L(E_n) = (K+1)(aE_0e^{-bE_0} - E_0) - (aE_ne^{-bE_n} - E_n) + (\text{terms depending on } E_0 \text{ and past escapements only}). \quad (6)$$

From Equation (6) it appears that the optimization will be over a total of $(K + 1)$ seasons. This is not actually the case since, as noted above, the constraint $E_{n+j} = E_0$ has been imposed and the analytical procedures used in year n will be applicable in year $(n + 1)$, etc. Note also the intuitively reasonable result that the loss given by Equation (6) is minimized by setting $E_n = E_0$, the optimum MSY escapement.

The analysis thus far has assumed that all quantities are deterministic. Random variables will now be introduced to simulate the situation actually existing in salmon fishery assessment and management. Let N_n denote the run size resulting from the (known) escapements $(E_{n-j})(j = 1, \ldots K)$ and let N_n be a random variable which, for definiteness, will be assumed to have the two-parameter gamma density

$$f_1(N_n \mid y_0) = \frac{\beta_0^{\alpha_0}}{\Gamma(\alpha_0)} N_n^{\alpha_0 - 1} e^{-\beta_0 N_n} \quad (7)$$

where Γ denotes a gamma function. The parameters (α_0, β_0) are subscripted to denote that they are applicable prior to the start of the run and f is subscripted by one to denote that it is applicable to the first fishing period. The quantity y_0 is a symbolic conditioning variable denoting the preseason information that is available for the specification of (α_0, β_0). Anticipating the dynamic nature of the fishery and its management the probability density of N_n will be conditioned successively to reflect the data obtained after the start of the run.

We assume now that the expected value, shown as $E[N_n]$ is that given by the Ricker relation, i.e.,

$$R_n = E[N_n] = a \sum_{k=1}^{K} p_k E_{n-k} e^{-bE_{n-k}}. \quad (8)$$

The variance of N_n may be estimated from historical data, e.g., smolt outmigrations, high seas catches, etc. Knowledge of the mean and variance is sufficient to determine the parameters (α_0, β_0).

At this point it might be well to justify, or at least explain, the assumption of a gamma density for N_n. Clearly, one cannot obtain Equation (7) on the basis of biological arguments. On the other hand, a gamma density does not do particular violence to one's intuition concerning the distribution of population sizes. In particular, Equation (7) confines N_n to positive values with scale and location specified by (α_0, β_0). In salmon population estimation, it is rare that parameters beyond mean and variance are available from whatever source. It is in this spirit that Equation (7) is introduced. Further, the gamma distribution, not coincidentally, has the added virtue that it is an analytically convenient function. Similar arguments will be used to justify some of the functions to be introduced subsequently.

For the remainder of the analysis, only events in year n will be considered so that the subscript may be omitted from N_n. The fishing season is assumed to consist of m nonoverlapping time periods during each of which a management decision, δ, must be made. Let (δ_i) $(i = 1, \ldots m)$ be an arbitrary sequence of decisions where each of the δ_i is a member of some finite set of possible management decisions.[3] Assume now that during the ith period a fraction ρ_i of the total run enters the fishery. The set $(\rho_i)(i = 1, \ldots m)$, which is assumed to be known, may be obtained from such sources as the almanac prepared by Royce (1965). The (ρ_i) must obviously satisfy the condition

$$\sum_{i=1}^{m} \rho_i = 1.$$

Corresponding to any actual realization of the run, N, there exists some unique set of optimum catch-escapement allocations (η_i) $(i = 1, \ldots m)$. Rothschild and Balsiger (1971) used linear pro-

[3]A typical set of management decisions consists of such actions as opening or closing the fishery, the imposition of gear limitations, waiting periods, etc.

gramming to determine an optimum set of such allocations. Such fine-scale is not practical here so that the individual η_i are irrelevant here except that they must satisfy the condition

$$N \sum_{i=1}^{m} \rho_i \eta_i = E_0.$$

Let $(\hat{\eta}_i)$ $(i = 1, \ldots m)$ be the actual allocations where each $\hat{\eta}_i$ will be assumed to be a random function of the management decision δ_i taken during the ith period. It will be assumed that the $(\hat{\eta}_i)$ $(i = 1, \ldots m)$ have independent beta distributions where the beta parameters (ν_i, μ_i) are uniquely determined by the management decision δ_i that is taken during period i. Thus we have

$$g(\hat{\eta}_1 \hat{\eta}_2 \ldots \hat{\eta}_m | \delta_1, \delta_2, \ldots \delta_m) = \prod_{i=1}^{m} g_i(\hat{\eta}_i | \delta_i) \quad (9a)$$

where

$$g_i(\hat{\eta}_i | \delta_i) = \frac{\Gamma(\nu_i + \mu_i)}{\Gamma(\nu_i)\,\Gamma(\mu_i)}\, \hat{\eta}_i^{\nu_i - 1} (1 - \hat{\eta}_i)^{\mu_i - 1}. \quad (9b)$$

This is a reasonable probability density to assume since it confines $\hat{\eta}_i$ to the interval (0,1) and the parameter choice permits, within appropriate limits, the specification of the mean and variance[4] of $\hat{\eta}_i$.

Return now to the central feature of the analysis which is to take into account the dynamics of the fishery. Equation (7) is the probability density of N appropriate for the first period of the fishery during which only preseason conditioning information, denoted symbolically by y_0, is available. Assume now that, during the first and subsequent time periods, additional population data, $y_1, y_2, \ldots$ become successively available. This data may then be used to condition the probability density of N, hopefully in such a manner that our knowledge of the true value of N, as measured by its variance, improves as more data are gathered. At each stage of the fishing season we compute the Bayes risk with respect to the then current probability density of N and adopt a strategy that takes into account all available data and all previous management decision. This will be formalized analytically upon the specification of an appropriate sampling distribution for the (y_i) $(i = 1, 2, \ldots m - 1)$. y_m is irrelevant since it is obtained after the final decision δ_m will have been made.

Assume that during each stage of the run some fixed fraction ϵ of the total number of fish entering the fishery is vulnerable to sampling. For example, if the sampling is done by gill nets ϵ may be determined from knowledge of the length, the time of soak, and the efficiency of the net. With such a sampling scheme, it is reasonable to assume that the samples $y_1, y_2, \ldots y_{k-1}$ will have independent Poisson densities with parameters λ_1, $\lambda_2, \ldots \lambda_{k-1}$ where $\lambda_i = \epsilon\rho_i N$, i.e., $\epsilon\rho_i N$ is the expected sample size for the ith period and

$$P(Y_i = y_i | N) = e^{-\epsilon\rho_i N} \frac{(\epsilon\rho_i N)^{y_i}}{y_i!} \quad (10)$$

where $y_i = 0, 1, \ldots$. Equation (10) and Bayes theorem may be utilized to modify or update Equation (7) to reflect the additional information that is assumed to have become available. Assume that the system is now at the start of the second stage and that the sample y_1 is now available. Bayes theorem gives

$$f_2(N | y_0, y_1) = \frac{P(Y_1 = y_1 | N) f_1(N | y_0)}{\int_0^\infty P(Y_1 = y_1 | N') f_1(N' | y_0) dN'}. \quad (11)$$

Substituting Equations (7) and (10) in Equation (11) gives, after dividing common factors,

$$f_2(N | y_0, y_1) = \frac{N^{\alpha_0 + y_1 - 1}\, e^{-(\beta_0 + \epsilon\rho_1)N}}{\int_0^\infty N^{\alpha_0 + y_1 - 1}\, e^{-(\beta_0 + \epsilon\rho_1)N} dN}. \quad (12)$$

The integral in the denominator of Equation (12) is a standard form expressible in terms of gamma functions which gives

$$f_2(N | y_0, y_1) = \frac{\beta_1^{\alpha_1}}{\Gamma(\alpha_1)} N^{\alpha_1 - 1} e^{-\beta_1 N} \quad (13)$$

where $\alpha_1 = \alpha_0 + y_1$ and $\beta_1 = \beta_0 + \epsilon\rho_1$. The updated probability density for N given by Equation (13) is, like the prior density given by Equation (7), a gamma density but with modified parameters α_1 and β_1. The process by which Equation (13) was obtained may be repeated indefinitely to give

$$f_k(N | y_0, y_1, \ldots y_{k-1}) = \frac{(\beta_{k-1})^{\alpha_{k-1}}}{\Gamma(\alpha_{k-1})} N^{\alpha_{k-1} - 1} e^{-\beta_{k-1} N} \quad (14)$$

[4]The conditioning of $\hat{\eta}$ by δ only is probably an oversimplification. There is evidence to indicate that $\hat{\eta}$ also depends on the number of fish that enter the fishery during any fishing period.

as the posterior density for N at the start of the kth fishing period. The parameters are given by $\alpha_{k-1} = \alpha_0 + y_1 + y_2 + \ldots + y_{k-1}$ and $\beta_{k-1} = \beta_0 + \epsilon(\rho_2 + \rho_2 + \ldots + \rho_{k-1})$. At this point it is appropriate to observe that, as time progresses and additional population data are obtained, the distribution of N, as specified by the parameters α_{k-1} and β_{k-1}, will more and more reflect the in-season sampling data with a corresponding decrease in the relevance of the preseason information implied by α_0 and β_0.

The probability densities given by Equations (7), (10), and (14) enjoy a peculiar relationship in which the posterior density of N, given by Equation (14), is from the same family as the prior density, Equation (7), for the particular sampling distribution given by Equation (10). Such pairs of densities are called conjugate pairs (DeGroot 1970:159-166). It is obvious that one cannot, in general, be so fortunate as to have parameter and sampling distributions that form a conjugate pair as in the model assumed here. However, DeGroot does outline some somewhat ad hoc procedures for constructing reasonable posterior probability densities.

All of the quantities and distributions necessary to compute the average or expected loss, i.e., the Bayes risk, are now available. The expression for the Bayes risk, to be evaluated at the start of the kth fishing period, may be written formally as

$$R_k(\delta_1, \delta_2, \ldots \delta_m \mid y_0, y_1, \ldots y_{k-1}) = \int_0^\infty f_k(N \mid y_0, y_1, \ldots y_{k-1}) dN \int_0^1 d\hat{\eta}_1 \cdots \int_0^1 d\hat{\eta}_m L(E_n) \prod_{i=1}^{m} g_i(\hat{\eta}_i \mid \delta_i) \quad (15)$$

where g_i, $L(E_n)$, and f_k are given by Equations (9), (6), and (14) respectively. Notice that the Bayes risk as given by Equation (15) is a function not only of the decisions already made, $\delta_1, \delta_2, \ldots \delta_{k-1}$ and the decision about to be made, δ_k, but of all future decisions $\delta_{k+1}, \ldots \delta_m$ as well. This dependence on all decisions, past, present, and future, reflects the assumption that the loss is a function primarily of the final state of the system, i.e., to a first approximation one cannot ascribe values to individual units of escapement during the season but only to the final total escapement. This presents no particular analytical difficulties since any particular sequence of optimum future decisions $\delta_{k+1}, \ldots \delta_m$ is certainly subject to revision as time passes and additional information becomes available.

Substituting Equations (6), (9), and (14) in Equation (15) gives

$$R_k(\delta_1, \delta_2, \ldots \delta_m \mid y_0, y_1, \ldots y_{k-1}) = \frac{(\beta_{k-1})^{\alpha_{k-1}}}{\Gamma(\alpha_{k-1})} \int_0^\infty N^{\alpha_{k-1}-1} e^{-\beta_{k-1}N} dN \int_0^1 d\hat{\eta}_1 \cdots \int_0^1 d\hat{\eta}_m \left\{ L'(E_0, E_{n-1}, \ldots E_{n-K}) - (aE_n e^{-bE_n} - E_n) \right\} \prod_{j=1}^{m} \frac{\Gamma(\nu_j + \mu_j)}{\Gamma(\nu_j)\Gamma(\mu_j)} \hat{\eta}_j^{\nu_j - 1} (1 - \hat{\eta}_j)^{\mu_j - 1} \quad (16)$$

where $L'(E_0, E_{n-1}, E_{n-2}, \ldots E_{n-K})$ denotes that portion of the loss function that does not depend on E_n. Thus L' is a fixed quantity and may be removed from the integral signs. This leaves only probability densities, which must integrate out to unity, so that

$$R_k(\delta_1, \delta_2, \ldots \delta_m \mid y_0, y_1, \ldots y_{k-1}) = L'(E_0, E_{n-1}, \ldots E_{n-K}) - \frac{(\beta_{k-1})^{\alpha_{k-1}}}{\Gamma(\alpha_{k-1})} \int_0^\infty N^{\alpha_{k-1}-1} e^{-\beta_{k-1}N} dN \int_0^1 d\hat{\eta}_1 \cdots \int_0^1 d\hat{\eta}_m (ae^{-bN\sum_{i=1}^{m} \rho_i \hat{\eta}_i} - 1) N \sum_{i=1}^{m} \rho_i \hat{\eta}_i \cdot \prod_{j=1}^{m} \frac{\Gamma(\nu_j + \mu_j)}{\Gamma(\nu_j)\Gamma(\mu_j)} \hat{\eta}_j^{\nu_j - 1} (1 - \hat{\eta}_j)^{\mu_j - 1} \quad (17)$$

where the escapement E_n has been expressed as

$$E_n = N \sum_{i=1}^{m} \rho_i \hat{\eta}_i .$$

The integrations in Equation (17) cannot be performed as expressed. If the order of the integrations is reversed, the integration with respect to N may be performed but the remaining integrations over $\hat{\eta}_1, \hat{\eta}_2, \ldots \hat{\eta}_m$ will be virtually impossible. However, if the exponential term $\exp\left(-bN \sum_{i=1}^{m} \rho_i \hat{\eta}_i\right)$ is expanded in its Maclaurin series and if the resulting multinomials of the form $\frac{1}{n!}\left(-bN \sum_{i=1}^{m} \rho_i \hat{\eta}_i\right)^n (n = 0, 1, \ldots)$ are expanded according to the multinomial theorem, the integrand in Equation (17) will be in a completely factored form. As a result of this factorization, the integrals take the form of various moments about

the origin. These integrals are all standard forms (c.f., Bierens de Haan 1939). The reader will be spared the details of this reduction and the ensuing integrations. The final expression for the Bayes risk is

$$R_k(\delta_1,\delta_2,\ldots\delta_m\,|\,y_0,y_1,\ldots y_{k-1})$$

$$= L'(E_0,E_{n-1},\ldots E_{n-K}) + \frac{\alpha_{k-1}}{\beta_{k-1}}\sum_{i=1}^{m}\frac{\rho_i\nu_i}{\nu_i+\mu_i}$$

$$-\frac{a}{\beta_{k-1}}\sum_{n=0}^{\infty}\left(-\frac{b}{\beta_{k-1}}\right)^n\frac{\Gamma(\alpha_{k-1}+n-1)}{n!\,\Gamma(\alpha_{k-1})}$$

$$\sum_{\Sigma k_i=n}^{k_i=0}\binom{n}{k_1k_2\ldots k_m}\sum_{i=1}^{m}\frac{\rho_i(\nu_i+k_i)}{\nu_i+\mu_i+k_i}$$

$$\cdot\prod_{j=1}^{m}\frac{\Gamma(\nu_j+\mu_j)\,\Gamma(\nu_j+k_j)}{\Gamma(\nu_j)\,\Gamma(\nu_j+\mu_j+k_j)}\,\rho_j^{k_j} \qquad (18)$$

where $\binom{n}{k_1k_2\ldots k_m}$ denotes a multinomial coefficient.

A slightly different form for the risk may be obtained under an alternate set of assumptions. Considerable emphasis has heretofore been placed on the conjugacy of the gamma-Poisson families of distributions. The gamma-Poisson assumption is a reasonable one and the resulting conjugacy lends a certain elegance. However, this line of analysis results in posterior gamma parameters (α_k, β_k) that, among other things, depend on the run fractions (ρ_i) $(i = 1, \ldots k)$. This parameter dependence on the run fractions virtually precludes treating the set (ρ_i) $(i = 1, \ldots k)$ as anything but fixed quantities; i.e., once a variable becomes the argument of a gamma function one has usually arrived at an analytical dead end. In actual practice, however, the quantities (ρ_i) $(i = 1, \ldots m)$ are random variables since there may be considerable year-to-year variation in the time profile of the run. Such temporal variation may be of considerable importance in Bristol Bay because of the large magnitude of the run and its short duration.

It has been suggested (O. A. Mathisen, pers. commun. and others) that the probability density of N is most appropriately conditional upon the catch-per-unit-effort (CPUE) observed during the course of the run. In so doing one can remove the explicit dependence of (α_k, β_k) on (ρ_i) $(i = 1, \ldots k)$. An implicit dependence remains, however, since the CPUE will be a function of the run fractions. One can formally bypass this dependence, however, by relating the density of N directly to the CPUE. In so doing one can then introduce temporal variability in the set (ρ_i) $(i = 1, \ldots m)$ and in evaluating the Bayes risk an additional expectation with respect to the density of these random variables must be taken.

An almost ideal probability density to describe the run fractions is the Dirichlet density defined by

$$h(\rho_1,\rho_2,\ldots\rho_m) = \frac{\Gamma(\gamma_1+\gamma_2+\ldots+\gamma_m)}{\Gamma(\gamma_1)\Gamma(\gamma_2)\ldots\Gamma(\gamma_m)}$$

$$\rho_1^{\gamma_1-1}\rho_2^{\gamma_2-1}\ldots\rho_m^{\gamma_m-1} \qquad (19)$$

where $\rho_i \geq 0$ for all i. As written this density is singular since the variates must satisfy the side condition $\sum_{i=1}^{m}\rho_i = 1$. The choice of the parameters $(\gamma_1, \gamma_2, \ldots \gamma_m)$ then permits the specification of any m of the means, variances, and covariances of the (ρ_i) $(i = 1, \ldots m)$. If Equation (19) is substituted in Equation (16) the integrations with respect to N and $(\hat{\eta}_1, \hat{\eta}_2, \ldots \hat{\eta}_m)$ may be done as before. The remaining integrals over $(\rho_1, \rho_2, \ldots \rho_m)$ are all Dirichlet integrals (Wilks 1962:177, et seq.) for which the values are readily determined. The resulting Bayes risk for this case may then be shown to be given by

$$R_k(\delta_1,\delta_2,\ldots\delta_m\,|\,\text{CPUE})$$

$$= L'(E_0,E_{n-1},\ldots E_{n-K}) + \frac{a\alpha_{k-1}}{G\beta_{k-1}}\sum_{i=1}^{m}\frac{\nu_i\gamma_i}{\nu_i+\mu_i}$$

$$-\frac{a}{\beta_{k-1}}\sum_{n=0}^{\infty}\left(-\frac{b}{\beta_{k-1}}\right)^n\frac{\Gamma(\alpha_{k-1}+n+1)}{\Gamma(\alpha_{k-1})\,\Gamma(G+n+1)}$$

$$\sum_{\Sigma k_i=n}^{k_i=0}\binom{n}{k_1k_2\ldots k_m}$$

$$\cdot\prod_{i=1}^{m}\frac{\Gamma(\nu_i+k_i)\,\Gamma(\nu_i+\mu_i)\,\Gamma(\gamma_i+k_i)}{\Gamma(\nu_i)\,\Gamma(\nu_i+\mu_i+k_i)\,\Gamma(\gamma_i)}$$

$$\sum_{j=1}^{m}\frac{(\gamma_j+k_j)(\nu_j+k_j)}{\nu_j+\mu_j+k_j} \qquad (20)$$

where $G = \sum_{i=1}^{m}\gamma_i$.

Equations (18) and (20) are somewhat intimidating, particularly if one were to attempt to infer the qualitative behavior of the system as the parameters descriptive of the fishery and its management are varied. Indeed, Equations (18) and (20) are virtually useless for this purpose with the exception of the determination of certain

limiting behavior as the appropriate parameters assume their extreme values. However, Equations (18) and (20) do have the virtue that, in closed form, the most crucial features of the fishery dynamics and statistics are accommodated in a quantitative and, hopefully, reasonably accurate fashion.

A NUMERICAL EXAMPLE

The foregoing mathematical model was applied to the simulated management of the Wood River system of Bristol Bay. It should be emphasized at the outset, however, that the assumptions, methods, and results presented here should in no way be construed as representing a management scheme preferable to those currently in use. The Wood River was chosen simply because, based on Mathews' (1966) data, it seemed to follow the Ricker spawner-return curve reasonably well.

In the example considered here, the model was limited to a fishing season of five time periods during each of which a choice of two management decisions was possible. This limitation was necessary to avoid inordinately lengthy calculations. Ricker parameter values of $a = 4.077$ and $b = 0.8 \times 10^{-6}$, which were used by Mathews, were used here. The return was assumed to consist of only the progeny of a single spawning group K years prior where K is arbitrary, i.e.,

$$p_i = \begin{cases} 1 & i = K \\ 0 & i \neq K \end{cases}.$$

All prior escapements were assumed to be the optimum escapement E_0 so that the loss function given by Equation (5) becomes

$$L_n = (aE_0e^{-bE_0} - E_0) - (aE_ne^{-bE_n} - E_n).$$

For the above values of the Ricker parameters, the MSY escapement is given by $E_0 = 709{,}000$. The expected value and standard deviation of a $\Gamma(\alpha_0, \beta_0)$ variate are given by α_0/β_0 and $\alpha_0^{1/2}/\beta_0$, respectively. In terms of the Ricker parameters, the expected run size is given by $aE_0 \exp(-bE_0)$ which determines the ratio $\alpha_0/\beta_0 = 1.64 \times 10^6$. An initial (i.e., preseason) standard deviation of one-half the expected run size was assumed. In terms of the gamma parameters this gives $\alpha_0^{1/2}/\beta_0 = \alpha_0/2\beta_0$ or $\alpha_0 = 4.0$ and $\beta_0 = 2.44 \times 10^{-6}$. The two management strategies assumed were complete closure (option 2) and one level of opening (option 1). In terms of the beta parameters, closure is simulated merely by setting $\mu_2 = 0$ with an arbitrary positive value for ν_2. During fishery opening it was assumed that an average of 80% of the available fish are caught with a standard deviation of 0.25. This gives $(\nu_1, \mu_1) = (0.312, 1.248)$ as the appropriate beta parameters. The set of run fractions (ρ_i) $(i = 1, \ldots 5)$ was determined from the time profile proposed by Royce (1965). Values of 0.156, 0.282, 0.348, 0.160, and 0.054, using five equal length time intervals, were obtained. No attempt was made to treat the run fractions as random variables. All of the parameter values were chosen to reflect reasonably well the known behavior of the system.

The fishery dynamics were treated by two distinct methods. The first method utilized the gamma prior density for N with a Poisson sampling density thus, through conjugacy, giving a gamma posterior density. A gamma posterior distribution was also assumed in the second method but the posterior gamma parameters were back-calculated after introducing prescribed stage-to-stage trends in the population mean and standard deviation.

The Bayes risk at each stage was computed for each of the $2^5 = 32$ total possible sequences of decisions, past, present, and future; i.e., no attempt was made to formulate and solve the functional equation associated with dynamic programming.[5] While relatively unsophisticated, this approach does permit one to use hindsight to determine, ex post facto, what an optimum previous strategy would have been, given the information currently available. In real life, of course, "what might have been" is irrelevant in the management of a dynamic system—one must optimize the system as it exists in real time in accordance with the principal of optimality, the relevant homily for which might well be "what's past is prologue."

The numerical results are summarized in Tables 1 to 3. Tables 1 and 2 give the optimum strategies and corresponding minimum Bayes risks for a gamma prior run size distribution with simulated

[5]Subsequent to the submission of this paper, C. J. Walters (1975) published a paper in which the ideas of dynamic programming were applied to the optimum year to year management of a salmon fishery. His work is of considerable interest, particularly since he managed to impose the principle of optimality and carry out the backward recursive scheme proposed by Bellman (1957). It remains to be seen if this method can be applied to the decision theoretic model presented here, but I am no longer as pessimistic as I formerly was.

TABLE 1.—Optimum strategies and minimum Bayes risks for a five-period, two-decision fishery with a sampling fraction $\epsilon = 1 \times 10^{-3}$.

Time period (i)	1	2	3	4	5
Run fraction (ρ_i)	0.156	0.282	0.348	0.160	0.054
Poisson parameter (λ_i)	256	462	570	262	—
$y_i = \lambda_i$					
Simulated samples (y_i)	256	462	570	262	—
Optimum strategy	open	open	close	open	open
Minimum Bayes risk	1.80×10^5	3.49×10^4	3.33×10^4	3.29×10^4	3.28×10^4
$y_i = 2\lambda_i$					
Simulated samples (y_i)	512	924	1,140	564	—
Optimum strategy	open	open	open	open	close
Minimum Bayes risk	1.80×10^5	1.89×10^5	1.70×10^5	1.90×10^5	1.90×10^5
$y_i = \frac{1}{2}\lambda_i$					
Simulated samples (y_i)	128	231	285	131	—
Optimum strategy	open	close	close	close	close
Minimum Bayes risk	1.80×10^5	6.90×10^3	3.35×10^3	2.48×10^3	2.29×10^3

TABLE 2.—Optimum strategies and minimum Bayes risks for a five-period, two-decision fishery with a sampling fraction $\epsilon = 1 \times 10^{-4}$.

Time period (i)	1	2	3	4	5
Run fraction (ρ_i)	0.156	0.282	0.348	0.160	0.054
Poisson parameter (λ_i)	26	46	57	26	—
$y_i = \lambda_i$					
Simulated samples (y_i)	26	46	57	26	—
Optimum strategy	open	close	open	open	open
Minimum Bayes risk	1.80×10^5	5.86×10^4	4.55×10^4	4.19×10^4	4.11×10^4
$y_i = 2\lambda_i$					
Simulated samples (y_i)	52	92	114	52	—
Optimum strategy	open	open	open	open	close
Minimum Bayes risk	1.80×10^5	1.86×10^5	1.87×10^5	1.89×10^5	1.88×10^5
$y_i = \frac{1}{2}\lambda_i$					
Simulated samples (y_i)	13	23	29	13	—
Optimum strategy	open	close	close	close	open
Minimum Bayes risk	1.80×10^5	4.14×10^4	1.85×10^4	1.12×10^4	9.65×10^3

TABLE 3.—Optimum strategies and minimum Bayes risks for a five-period, two-decision fishery with linear stage-to-stage trends in the expected run size and the run size standard deviation with preseason parameters $\alpha_0 = 4.0$ and $\beta_0 = 2.44 \times 10^{-6}$.

Time period (i)	1	2	3	4	5
Run fraction (ρ_i)	0.156	0.282	0.348	0.160	0.054
Constant expected run size:					
α_{i-1}/β_{i-1}	1.64×10^6	1.64×10^6	1.64×10^6	1.64×10^6	1.64×10^6
$\sqrt{\alpha_{i-1}}/\beta_{i-1}$	8.20×10^5	6.89×10^5	5.57×10^5	4.26×10^5	2.95×10^5
Optimum strategy	open	close	open	open	open
Minimum Bayes risk	1.80×10^5	1.41×10^5	1.07×10^5	7.87×10^4	5.74×10^4
Increasing expected run size:					
α_{i-1}/β_{i-1}	1.64×10^6	1.97×10^7	2.30×10^6	2.63×10^6	2.95×10^6
$\sqrt{\alpha_{i-1}}/\beta_{i-1}$	8.20×10^5	6.89×10^5	5.57×10^5	4.26×10^5	2.95×10^5
Optimum strategy	open	open	open	close	open
Minimum Bayes risk	1.80×10^5	1.40×10^5	1.26×10^5	1.43×10^5	1.90×10^5
Decreasing expected run size:					
α_{i-1}/β_{i-1}	1.64×10^6	1.48×10^6	1.31×10^6	1.15×10^6	9.84×10^5
$\sqrt{\alpha_{i-1}}/\beta_{i-1}$	8.20×10^5	6.89×10^5	5.57×10^5	4.26×10^5	2.95×10^5
Optimum strategy	open	open	close	close	close
Minimum Bayes risk	1.80×10^5	1.52×10^5	1.25×10^5	9.57×10^4	6.68×10^4

Poisson sampling. The sampling was intended to simulate actual run sizes equal to, greater than, or less than the preseason estimate of the run size, α_0/β_0. The Poisson sampling was done by brute force in which sample values exactly equal to the desired expected values were chosen. For example, to simulate an actual run size twice that based on the preseason parameters we choose $y_i = 2\lambda_i$ where $\lambda_i = \epsilon\rho_i\,\alpha_0/\beta_0$ is the Poisson parameter for the ith period obtained from the preseason parameters. The deterministic samples (which is really a contradiction in terms) permit one to elicit the response of the system to specified input stimuli.

The Bayes risks are all in units of numbers of fish. The optimum strategy is that strategy which

minimizes the Bayes risk given that all prior decisions were optimum for the time periods in which they were made. In other words, the "hindsight" feature was not utilized to "improve" a past decision—once made any decision is retained through all subsequent stages.

The mathematical machinery developed generally gives intuitively reasonable results. Specifically, the tendency toward larger or smaller run sizes results in optimum strategies that tend successively toward more or fewer open periods respectively. The Bayes risk generally, but not always, decreases as the season progresses, largely reflecting the decreasing variances in the estimates of the run size. Increases in the Bayes risk can usually be attributed to past decisions that, in the light of subsequent sampling, are no longer optimum thus requiring corrective action.

CONCLUSIONS

The mathematical models assumed and developed here for the objective management of a typical salmon fishery, as previously noted, are based on quite specific functional forms and thus represent somewhat of an idealized situation. However, these functions were chosen to reflect the behavior of the system insofar as the knowledge of such behavior is available. Indeed, the acquisition of such detailed knowledge is an important area of current research and subsequent refinements of the statistics will be possible as more data are gathered.

Of more concern than the accuracy of the fine-scale mathematical behavior of the system is the appropriateness of the basic mathematical theory upon which the models are built. I feel that statistical decision theory is a most natural framework on which to base an objective management model. The nomenclature lends support to this view. For example, the equivalence of a management decision and a statistical decision is obvious.[6] The term risk, in the economic if not the strict Bayesian sense, is frequently used in discussions of fishery management. Finally, Bayes theorem provides a convenient and theoretically appropriate method for accommodating the combined data acquisition and dynamics of the fishery.

Advantage has been taken of some powerful analytical tools to characterize salmon fishery management. However, any enthusiasm for these quite contemporary methods should be tempered somewhat by consideration of some of the specific practical difficulties likely to be encountered. One of these, mentioned in Lord (1973), is the difficulty associated with multistage dynamic processes. While the fishery management problem under discussion falls very naturally into a class of stochastic dynamic programs it is not yet obvious whether the functional equation arising from the imposition of the principal of optimality can be formulated or solved in a useful fashion. The calculations done here were more of the brute force variety in which all strategy combinations, optimal or not, were considered. In other words, the backward recurrence scheme central to dynamic programming was not used to reduce the total number of possible strategies to be considered. In so doing, the "Curse of Dimensionality," about which Bellman (1957:6) so aptly warned, proved to be a limiting condition. To evaluate completely the five-stage, two-decision fishery considered here required from 10 to 15 min of Control Data Corporation[7] 6400 central processor time for each set of input parameters. This is not a trivial numerical effort and should give one pause when considering more elaborate models.

In conclusion I feel that advantage should be taken of the appropriate analytical tools as they are made available by the mathematicians or, at the very least, such tools should be investigated. However, the availability of such methods in no way indicates their eventual practicality for any specific problem. For this careful additional investigation is necessary.

LITERATURE CITED

BELLMAN, R.
1957. Dynamic programming. Princeton Univ. Press, 340 p.

BIERENS DE HAAN, D.
1939. Nouvelles tables d'intégrules définies. G. E. Stechert & Co., 716 p.

DEGROOT, M. H.
1970. Optimal statistical decisions. McGraw-Hill Book Co., Inc., 489 p.

LORD, G. E.
1973. Characterization of the optimum data acquisition and management of a salmon fishery as a stochastic dynamic program. Fish. Bull., U.S. 71:1029-1037.

[6]This equivalence is not always evident even within decision theory itself. For example, it requires a slight mental contortion to treat statistical estimation as an application of decision theory as the statisticians have done.

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

MATHEWS, S. B.
1966. The economic consequences of forecasting sockeye salmon (*Oncorhynchus nerka*, Walbaum) runs to Bristol Bay, Alaska: A computer simulation study of the potential benefits to a salmon canning industry from accurate forecasts of the runs. Ph.D. Thesis, Univ. Washington, Seattle, 238 p.

ROTHSCHILD, B. J., AND J. W. BALSIGER.
1971. A linear-programming solution to salmon management. Fish. Bull., U.S. 69:117-140.

ROYCE, W. F.
1965. Almanac of Bristol Bay sockeye salmon. Univ. Wash. Fish. Res. Inst. Circ. 235, 48 p.

WALTERS, C. J.
1975. Optimal harvest strategies for salmon in relation to environmental variability and uncertain production parameters. J. Fish. Res. Board Can. 32:1777-1784.

WILKS, S. S.
1962. Mathematical statistics. John Wiley & Sons, Inc., N.Y., 644 p.

DIEL CHANGES IN SWIM BLADDER INFLATION OF THE LARVAE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

JOHN R. HUNTER AND CAROL SANCHEZ[1]

ABSTRACT

Laboratory and field studies demonstrated that larval anchovy 10 mm standard length and larger inflate their swim bladders each night and deflate them in the day. Maximum night levels of inflation were attained 2 h after the onset of dark and typical day levels occurred about 2 h after the onset of light. Laboratory experiments indicated that larvae fill their bladders at night by swallowing air at the water surface and the vertical distribution of sea-caught larvae suggested that they migrate to the surface each night to fill their swim bladders. Gas is released by passing bubbles through the pneumatic duct into the alimentary canal. The diel rhythm of inflation was viewed as an energy sparing mechanism. Measurements of sinking speed of larvae with and without inflated bladders suggested that the energy saved at night by inflation of the swim bladder would exceed the cost of vertical migration to the surface and that the migratory range over which energy savings are possible would be greater as larvae increased in length.

Northern anchovy, *Engraulis mordax* Girard, are more vulnerable to starvation in the larval stage than at any other time of life, consequently, energy sparing mechanisms may be critical to their survival. In a recent paper Uotani (1973) showed that the larvae of several clupeoid fishes, *Engraulis japonicus* (Houttuyn), *Sardinops melanosticta* (Temminck and Schlegel), and *Etrumeus teres* (DeKay) have expanded swim bladders when captured at night in the sea and deflated ones when captured during the day. Energy conservation is certainly one of the possible adaptive advantages of such behavior, but the energy saved must be evaluated in terms of the energy cost of daily filling the bladder. This requires that the mechanism of filling be known. The object of the present study was to determine if the larvae of the northern anchovy display a similar rhythm and to evaluate this behavior as a possible energy sparing mechanism.

The swim bladder in adult northern anchovy is a tubular vesicle that extends the length of the body cavity. It is connected to the alimentary canal by a pneumatic duct which originates from the dorsal wall of the cardiac stomach; no anal duct exists as it does in some clupeoids (O'Connell 1955). Two tubules on each side of the body extend from the anterior end of the bladder into the cranium where they expand into two pairs of capsules, termed prootic and pterotic bullae (O'Connell 1955). The swim bladder of the larva is basically similar to that of the adult. At the time of initial filling of the swim bladder, the pneumatic duct is functional and the bullae become filled with gas. No histological evidence exists for gas secretion in adult *E. mordax* nor for the larvae (O'Connell 1955, and pers. commun.).

The swim bladder is deflated by passing gas bubbles through the pneumatic duct into the alimentary canal and out the anus. On a number of occasions we have observed this process while examining a live anchovy larva under a dissection microscope. We have also captured larvae with deflated swim bladders that had gas bubbles in the alimentary canal.

METHODS

Fertilized anchovy eggs were obtained from a captive population of adults maintained in spawning condition in the laboratory (Leong 1971) and the larvae were reared using the techniques, foods, and tanks described by Hunter (1976). The larvae were reared at temperatures of 16.5° ± 0.2°C and 16.9° ± 0.9°C. A 12-h photoperiod was used without a dawn or dusk transition in light intensity. Incident light at the surface was about 2,000 lx in the day and at night no light was provided in the closed room which contained the rearing tanks.

Larvae reared in the laboratory were sampled at

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various times of day commencing at age 1 day to determine if a daily rhythm of inflation existed and to determine the larval length at which the swim bladder was inflated. Samples of preserved specimens from California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton collections were also examined to determine if differences existed in swim bladder inflation in sea-caught specimens.

The standard length was measured to the nearest 0.1 mm and the maximum width and length of the swim bladder to the nearest 0.02 mm. The volume of the swim bladder was calculated by using the equation for a prolate spheroid, $V = 4/3\pi ab^2$, where a is half the maximum bladder length and b is half the maximum width. For larvae 16 mm and larger, the calculated swim bladder volume may be converted to actual gas volume by multiplying it by the coefficient 0.82 (Figure 1). This conversion is based on data obtained while measuring the composition of swim bladder gas. The larvae used in that experiment were larger (mean length 15.6 to 29.6 mm) than most of the larvae in the rest of the experiments. For this reason we have used the calculated swim bladder volume in all computations.

We also sampled larvae reared in the laboratory to determine the effect of swim bladder development and swim bladder inflation on sinking rate. The method of Blaxter and Ehrlich (1974) was used to measure sinking rates of larvae. Larvae anesthetized in MS 222[2] were measured and added to a 1-liter graduated cylinder without contact with the air. The larvae were allowed to sink a few centimeters, then the rate of descent was timed with a stopwatch for a distance of 7 to 35 cm. Only one measurement was made per larva and larvae were reexamined after the test to determine if they were still alive (dead larvae sank faster than live ones) and if any gas had been lost from their bladders. Fresh seawater was used in the graduated cylinder for each day's run and the specific gravity and temperature of the seawater were measured before each larva was tested. The specific gravity averaged 1.0262 and ranged from 1.0259 to 1.0266. The graduated cylinder was immersed in a temperature-controlled water bath which was maintained within 1°C of the rearing temperature. One rearing group was tested at 15.9° ± 0.2°C and another at 18.0° ± 0.1°C. In the Results section we have combined the data from these two rearing groups because covariance analysis indicated that the differences in sinking speed when adjusted for swim bladder volume and larval length were not significant.

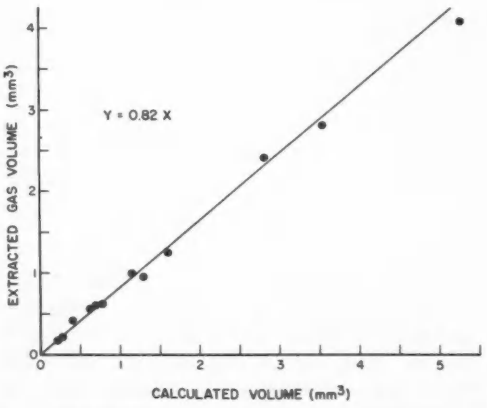

FIGURE 1.–Relation between the volume of the swim bladder calculated from the equation $V = 4/3\pi ab^2$ and the actual volume of gas extracted from the swim bladder for northern anchovy larvae of mean length 15.6 to 29.6 mm. Each point is the mean volume of the swim bladder calculated for a sample of two to eight larvae taken at night and the average volume of gas extracted from that sample. Sample means were weighted by their variances to calculate the regression line; intercept for line did not differ from 0; and the standard error of line was 0.0428.

To determine if anchovy larvae filled the swim bladder by gulping air at the water surface, the following experiment was performed. Commencing 4 h after the onset of dark, larvae in a 400-liter rearing tank were sampled and the lengths and dimensions of the swim bladder of each larva in the sample measured. Just before the onset of dark on the following day, the surface of the tank was sealed with a 0.5-cm layer of mineral oil. A second sample was taken commencing at 2400 h, 4 h after the onset of dark and ending just before the beginning of light at 0800. A third sampling was taken of larvae in the sealed tank during the day beginning at 1000 h, 2 h after the onset of light, and ending at 1400.

The gas content of the swim bladders of laboratory-reared larvae captured in the dark was analyzed using the micro gasometric method and apparatus described by Scholander et al. (1955). Swim bladders were dissected from the larvae in acid citrate solution, removed with a Pasteur pipette, and injected into an acid citrate filled capillary tube sealed at one end. After two to eight

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

swim bladders had been collected, they were macerated in the tube and the gas withdrawn with a Pasteur pipette and inserted into the syringe gas analyzer (Scholander et al. 1955). In the analyzer, the carbon dioxide was absorbed with alkaline citrate, oxygen by pyrogallol, and the volume of gas determined before and after each treatment. The remaining gas was considered to be nitrogen. The volume of gas was read under a dissecting microscope using an optical micrometer. Reading error was about ± 0.09 µl or from 1 to 2% depending on the volume of the sample.

RESULTS

Diel Rhythm in Swim Bladder Inflation

The volume of the swim bladder of larvae captured at night in the sea was greater than that of larvae collected in the day (Table 1). Similarly, the volume of the swim bladder of larvae reared in the laboratory was greater at night than in the day. To illustrate these daily changes for laboratory-reared larvae, the mean volume of the swim bladder for 2-h intervals was calculated for each of three length classes (10.0 to 11.9 mm, $N = 121$; 12.0 to 13.9 mm, $N = 202$; 14.0 to 15.9 mm, $N = 129$). No evidence existed for anticipation of the onset of dark at 2200 h nor for the onset of light at 1000 h (Figure 2). In all three length classes the mean volume did not return to the daytime level until about 2 h after the onset of light nor did they reach the maximum at night until about 2 h after the onset of dark.

The swim bladder of larvae at night was frequently so inflated that it constricted the gut (see fig. 8 in Uotani 1973). Larvae in the dark with filled swim bladders were motionless or slowly sinking. The body was oriented head down at an oblique angle to the water surface. After sinking a short distance, the larvae swam back to the water surface, a behavior closely resembling that of yolk-sac larvae (Hunter 1972).

Specimens with obviously inflated swim bladders occurred occasionally in day samples from the sea and laboratory but these were only a few percent of the larvae examined if the first 2 h after the onset of light are excluded. On the other hand, the occurrence of larvae with deflated bladders at night was more common. About 10% of the wild larvae and 20% of the laboratory-reared (12.0 to 12.9 mm) larvae had swim bladder volumes at night comparable to those in the day (Figure 3). The proportion of larvae with deflated bladders at night decreased with larval length.

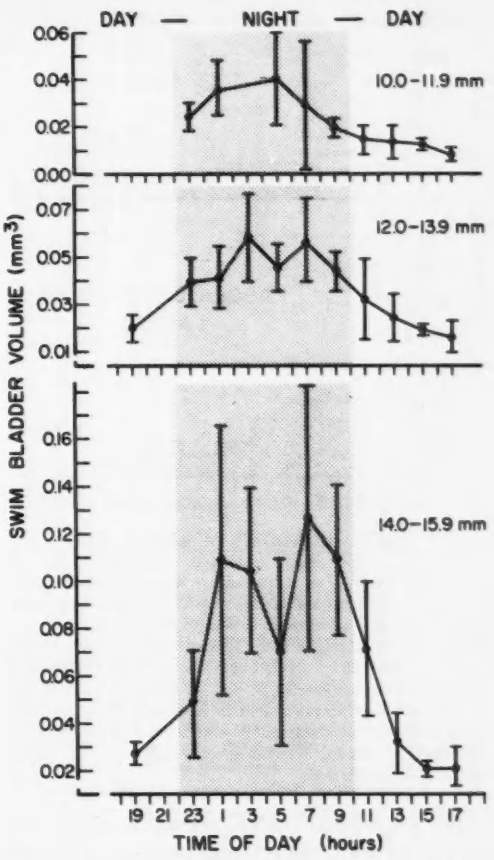

FIGURE 2.–Mean swim bladder volume ± 2 SE of mean for 2-h class intervals plotted at midpoint of each 2-h class. Data shown for three length classes of laboratory-reared northern anchovy larvae; the onset of dark was at 2200 h and onset of light at 1000 h. No transitional level of illumination existed between night and day.

TABLE 1.–Swim bladder volume (mm³) of preserved northern anchovy larvae from standard CalCOFI oblique plankton tows taken at night and in the day in southern California inshore waters.

Length class (mm)	Night samples		Day samples	
	N	Swim bladder vol (mean ± 2 SE)	N	Swim bladder vol (mean ± 2 SE)
11.0-11.9	23	0.044 ± 0.007	28	0.016 ± 0.008
12.0-12.9	20	0.073 ± 0.015	30	0.015 ± 0.004
13.0-13.9	24	0.124 ± 0.011	17	0.030 ± 0.016
14.0-14.9	14	0.128 ± 0.011	6	0.029 ± 0.003

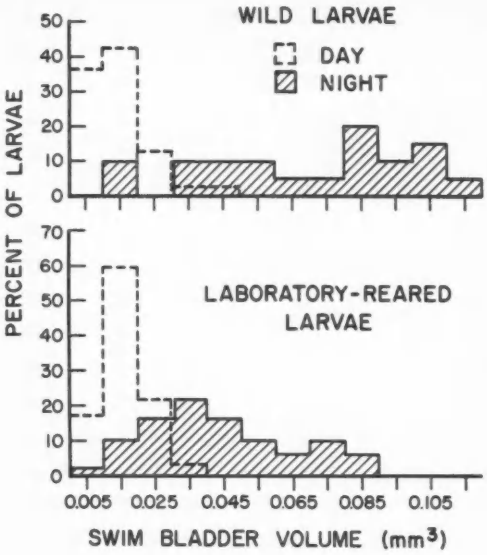

FIGURE 3.–Percent of northern anchovy larvae, 11.9 to 12.0 mm, at night (solid bars) and in day (dashed bars) having swim bladder volumes in various 0.01-mm^3 classes; numbers on abscissa are midpoints of swim bladder volume classes. Upper panel, larvae from CalCOFI ichthyoplankton collections (preserved specimen length), N = 20 for night, and N = 30 for day. Lower panel, larvae reared in laboratory (live specimen length), N = 49 for night, and N = 29 for day. Data from 2-h after onset of dark and 2-h after onset of light were excluded in laboratory-reared larvae.

The mean swim bladder volume at night was greater for wild than for laboratory-reared larvae of the same length. The effect of preservation on larval length for larvae of this size is not known but a shrinkage of about 10% in length in the Formalin-preserved ichthyoplankton specimens would account for this difference. The effect of preservation on swim bladder volume is also unknown. In some of the preserved specimens, we noticed the bladder was filled with fluid but we did not routinely make an examination of the bladder contents.

Swim Bladder Inflation and Larval Length

The swim bladder was fully formed when larvae reached 8 to 9 mm but it usually was not inflated. To determine the larval size at which nightly inflation commenced, night and day samples from the laboratory were grouped into 1-mm length classes (9.0 to 9.9 mm, 10.0 to 10.9 mm, etc.), and the mean volume for day and night samples for each class calculated, and compared using the t test. The first 2 h after the onset of dark and the onset of light were excluded from the classes.

Some of the 9.0 to 9.9 mm larvae appeared to have inflated swim bladders at night but the night-day difference in swim bladder volume was not significant ($0.2>P>0.1$). Mean volumes for day and night samples were different in larvae 10.0 to 10.9 mm as were those for larvae in all succeeding length classes ($P<0.001$). Thus, the threshold larval length for nightly inflation of the swim bladder occurred at about 10 mm, the point at which the means for day and night volumes diverge (Figure 4).[3] From this point, mean volume of night samples increased exponentially with length whereas that for day samples increased linearly.

Relation Between Sinking Speed, Swim Bladder Volume, and Larval Length

We observed that larvae with inflated bladders sank more slowly than those with uninflated

[3]Swim bladder inflation is reported to occur at 7 mm in *E. japonicus* (Uotani 1973). Comparison of his illustrations to those of Uchida et al. (1958) suggests Uotani's reported lengths are in error and that *E. japonicus* also inflates the bladder at about 10 mm.

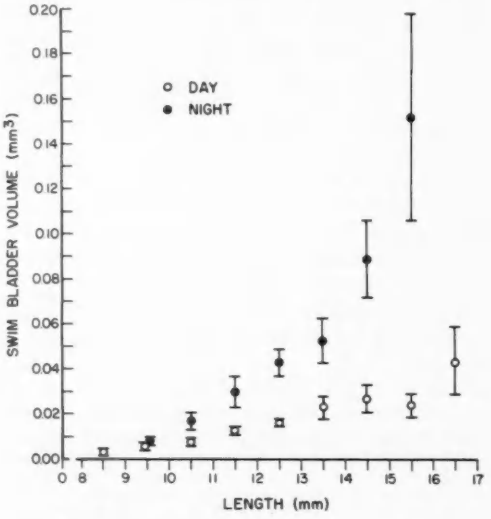

FIGURE 4.–Mean swim bladder volume ± 2 SE for laboratory-reared northern anchovy larvae for 1-mm classes of length plotted at the midpoint of each class. Solid circles are night (first 2-h after onset of dark omitted) and open circles day (first 2-h after onset of light omitted).

bladders. At night, larvae were occasionally neutrally buoyant but most were slightly negatively buoyant.

To develop an equation for expressing sinking speed in terms of larval length and swim bladder volume, the data on sinking speeds were grouped into four classes of larval length: 10.0 to 11.9 mm, $N = 30$; 12.0 to 13.9 mm, $N = 41$; 14.0 to 15.9 mm, $N = 54$; and 16.0 to 17.9 mm, $N = 14$. A regression of sinking speed on swim bladder volume for each length class yielded the following slopes and standard errors for the regression lines: -3.040, SE = 2.339; -4.001, SE = 1.297; -4.8796, SE = 0.616; and -5.070, SE = 1.680, respectively. Covariance analysis of these data indicated that the slopes were not different whereas the intercepts for the regression lines were statistically different ($P = 0.01$). Since no difference existed in the slopes among the four groups, the common slope from the covariance analysis, -4.769, SE = 0.487, was used to express the relation between sinking rate and swim bladder volume for each length class (Figure 5, lower panel). When adjusted for the common slope, the sinking rate intercepts of the four regression lines showed a precise linear relationship when plotted against the midpoints of their respective length classes (Figure 5, upper panel). The equation for the intercept-length relationship was $y = 0.18L - 1.51$ where L is larval length (the midpoints of the larval length classes) and y is the intercept for the regression of sinking rate on swim bladder volume (the sinking rate at $V = 0$ in Figure 5). This equation was combined with the common slope to provide the equation given below:

$$S = 0.18L - 1.51 - 4.77V$$

where S = sinking speed in centimeters per second
L = larval length in millimeters
V = swim bladder volume (outside dimensions) in cubic millimeters.

We examined the changes in sinking speed of larvae from the time of hatching through the development of the swim bladder. These changes are of interest because they illustrate the timing of swim bladder development, its effect on buoyancy, and the advantage of a nightly inflation cycle. Data for sinking rates for larvae 4.0 to 9.9 mm were grouped into 1-mm classes and the means plotted at the midpoints of the class intervals except for the yolk-sac larvae (3.7 mm) which were all about the same length. For larvae 10.0 mm or larger, we calculated sinking speeds from the mean swim bladder volume given in Figure 4 using the equation given in the preceding paragraph.

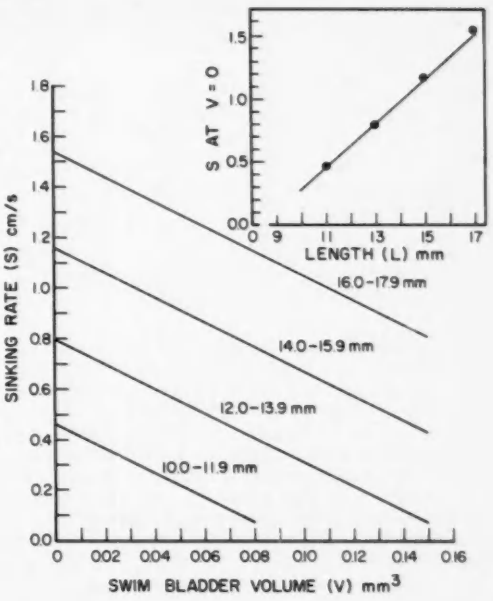

FIGURE 5.—The relation in larval northern anchovy between sinking speed (S), swim bladder volume (V), and larval length (L). Lower panel, regression lines show relation between sinking speed and swim bladder volume for the four classes of larval length indicated in the figure, when a common slope of -4.769 is used (see text). Upper panel, the regression of the y intercepts (S at $V = 0$) of the four regression lines on larval length (midpoints of the four length classes); equation for intercept line was $y = 0.18L - 1.51$. Final equation is $S = 0.18L - 1.51 - 4.77V$.

Sinking speed increased exponentially with length, when larvae sampled at night are excluded (Figure 6). The increase is roughly proportional to the cube of the length (curved line in Figure 6). This might be expected since sinking speed is dependent upon buoyancy which varies with the volume (L^3) and the difference in specific gravity between the fish and its medium. For estimating mean sinking speed for larvae with swim bladders in the day, or for those without swim bladders the equation $S = 0.094 + 0.000264L^3$ where L is length in millimeters and S is sinking speed in centimeters per second, gives a good fit to the data.

The length threshold for filling the swim bladder (about 10 mm) coincides with a rapid acceleration

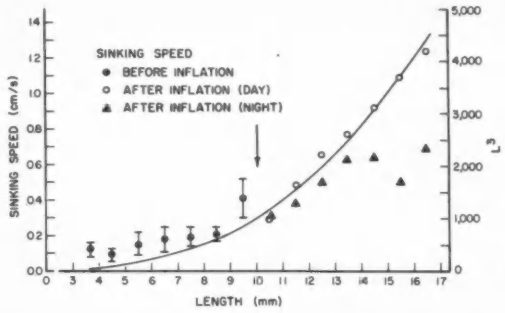

FIGURE 6.–Change in sinking speed from hatching through threshold of the initial inflation of swim bladder (arrow) of northern anchovy larvae. For larvae <10 mm, mean sinking speed ± 2 SE were plotted against the midpoint of 1-mm length classes, except for the first point which was for yolk-sac larvae and is plotted at average length for the class. For larvae >10 mm, sinking rates are estimated from the mean swim bladder volume given in Figure 3 using the general equation for sinking speed given in Figure 5. Open circles are estimates for the day and solid triangles for the night. Line is the cube of the length (L^3) plotted against length.

in the volume of the larva and its sinking speed. Thus, the timing of the swim bladder inflation may be related to these events.

The effect of night inflation of the swim bladder is also illustrated in Figure 6. For larvae 12 mm and larger, the average sinking speed at night appears to be relatively constant at about 0.6 ± 0.1 cm/s (22 m/h) while the sinking speed in the day increased exponentially with length. A larva 16.5 mm long had a sinking speed at night nearly half that of the day. Swimming speeds of larval anchovy while searching for food in the day, range from about 0.6 to 1.0 body length/s (Hunter in press). If a larva did not inflate the swim bladder at night, the swimming required just to maintain a position in the water would be equivalent to that used in the search for food in the day. Since larvae do not feed at night, filling the swim bladder would clearly be advantageous as an energy conserving mechanism.

Mechanism of Swim Bladder Inflation

It was not possible to determine if larvae in the tank sealed with mineral oil swam just below the layer of oil or into it because our view was from above rather than from the side. However, the mean swim bladder volume for larvae sampled at night in the sealed tank was less than that for larvae sampled on the previous night when the tank was not sealed (t test, $P = 0.001$, Table 2). The mean volumes of the swim bladders for larvae in the day and at night in the sealed tank were not different. This experiment suggests that anchovy larvae in the laboratory fill their swim bladders by swallowing air at the surface.

TABLE 2.–Mean swim bladder volume and mean length of northern anchovy larvae in sealed and unsealed containers.

Treatment	N	Mean length of larvae (mm ± 2 SE)	Mean swim bladder vol (mm^3 ± 2 SE)
Unsealed tank:			
Night	12	13.9 ± 0.37	0.094 ± 0.037
Sealed tank:			
Night	18	14.1 ± 0.41	0.035 ± 0.008
Day	17	13.8 ± 0.86	0.026 ± 0.019

An analysis of the oxygen content of the swim bladder could suggest whether or not the gas in the swim bladder was secreted or taken from the air. Newly secreted gas would be expected to be oxygen (Wittenberg 1958), but if larvae were swallowing air the concentration should be about 21% oxygen. Our analysis did not agree with either pattern even though some measurements were made 30 min after the onset of dark. Samples averaged about 11% oxygen, consistently less than the atmospheric concentration (Table 3). Carbon dioxide levels (0.9 to 2.2%) were higher than atmospheric levels but little can be concluded because our experimental reading error was 1 to 2% owing to the small volumes used. It is probable that oxygen was lower than atmospheric concentration because it was absorbed from the bladder by the larva. Except for the first two observations in Table 3, oxygen concentration tended to decrease with time from the onset of dark. It should be noted that preferential removal of oxygen from swim bladder gases is not unique to anchovy larvae but is found in most fishes which have been studied (Wittenberg 1958).

The rate at which the swim bladder was filled also suggests that the filling is accomplished by gulping air. Larvae with filled swim bladders were captured 20 to 30 min after the onset of dark and the means were at a maximum by 2 h after dark. Uotani (1973) reported for *E. japonicus* that filling was completed by 1 h in the sea. Fishes that fill the swim bladder by secretion require much more time to fill the bladder, for example, *Stenotomus versicolor* (Mitchill) requires 10 to 12 h; *Anguilla rostrata* (LeSueur), 12 to 24 h; *Opsanus tau* (Linnaeus), *Prionotus carolinus* (Linnaeus), and *P. evolans* (Linnaeus), 24 h; and *Tautoga onitis*

TABLE 3.—Percent composition of swim bladder gas of laboratory-reared northern anchovy larvae sampled at night, listed in order of time of sampling.

Elapsed time after onset of darkness (h)	(min)	Number of larvae	Mean larval length (mm)	Composition of swim bladder gas (%) CO_2	O_2	N_2	Sample volume (μl)	Oxygen in tank (ml/liter)
0	30	2	27.1	1.2	9.6	89.2	5.54	5.4
0	30	2	29.6	1.6	8.2	90.2	8.12	—
0	50	4	22.1	1.3	14.2	84.5	4.99	5.7
3	15	5	21.0	1.8	13.1	85.0	6.08	5.0
4	20	3	25.3	2.2	11.1	86.7	7.18	5.1
6	25	8	19.3	0.9	12.7	86.4	4.85	4.6
6	25	7	18.9	0.6	12.6	86.9	4.05	5.0
7	35	6	22.1	1.4	9.1	89.5	6.06	4.9
8	10	6	20.1	0.6	9.5	89.9	3.70	4.8

Linnaeus, about 24 h (Wittenberg 1958). Considering the evidence presented here, and the apparent lack of gas secretion in clupeoid fishes in general (Brawn 1962), the most tenable hypothesis is that swim bladder inflation is accomplished in larval anchovy by taking in air at the water surface.

Vertical Migration

If anchovy larvae fill their swim bladders each night by swallowing air, they must either remain near the surface throughout the day and night or migrate to the surface at dusk.

We reexamined the original data collected by Ahlstrom (1959) to determine if any evidence existed for vertical movements in northern anchovy larvae. Ahlstrom (1959) made extensive horizontal tows for fish larvae with opening and closing nets and presented the average number of larvae of all lengths at various depths. We separated his original length data into two length classes: larvae <11.75 mm (preserved standard length) and larvae ≥11.75 mm for night and day collections; we omitted those collections occurring near dawn and dusk. Unfortunately, only 14 larvae ≥11.75 mm were taken in the day while 279 were taken at night but the depth pattern in the day collections was relatively consistent. Larvae <11.75 mm were more abundant: N = 6,456, night; and N = 331, day.

At night, over 50% of the larvae ≥11.75 mm were taken in the upper 10 m whereas in the day the upper 10 m contained less than 10% of the larger larvae (Figure 7). About 50% of the larvae <11.75 mm occurred in the upper 10 m, but no obvious difference between day and night samples existed. These results are in general agreement with those of Ida (1972) who studied the vertical distribution of the Japanese anchovy, *E. japonicus*, a closely related species that also has a diel rhythm in swim bladder inflation (Uotani 1973). Ida (1972) found a striking diel change in the vertical distribution of *E. japonicus* with the maximum numbers occurring at the surface at night and at 20 to 30 m during the day with the movement to the surface occurring at twilight. Examination of the size frequency histograms from some of the collections

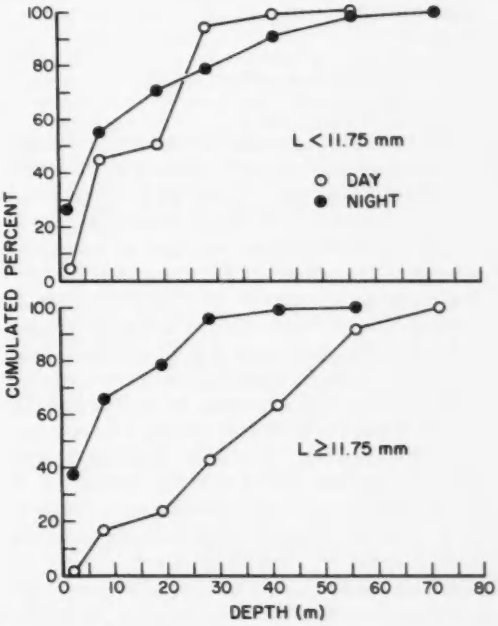

FIGURE 7.—The vertical distribution in the sea of northern larvae at night and in the day for two length classes; length <11.5 mm, upper panel, and length ≥11.5 mm, lower panel (lengths for preserved specimens). Numbers of larvae taken at each depth were cumulated starting at the shallowest tow (5 m) and expressed as the cumulated percent of the total larvae taken. Data are from Ahlstrom (1959).

led Ida to conclude that the diurnal change was caused by the vertical migration of the larger larvae (10 to 15 mm).

The diel vertical movements that appear in larval anchovy at the time of swim bladder inflation probably persist into adult life. The adults, however, are quite variable in their behavior which changes with size of school and season (Mais 1974). Vertical migration is most noticeable in large schools which are deep during the day (119 to 220 m) and rise to the surface and disappear as sonar targets at dusk. These schools reform and descend at first light in the morning (Mais 1974).

Possible Adaptive Advantages

Inflation of the swim bladder reduces the energy required for maintaining a position in the water column. This reduction in sinking speed could represent an important energy savings for larval anchovy because they do not feed at night and swimming can not be used in the search for food. The major energy cost of a diel rhythm of swim bladder inflation is the required vertical migration to the surface. Laboratory work suggests that anchovy larvae, by modification of swimming speed and direction of turning, are able to find and remain in area of high food density (Hunter and Thomas 1974). Thus, it is possible that a larva could follow an upward and downward movement of food at dusk and dawn. In this case the added cost for vertical movements would be slight since the energy spent in swimming could be used in searching for food. It is unlikely, however, that this condition could always be met. Thus, the energy saved at night by inflation of the swim bladder should exceed that used in vertical migration. Assuming the energy used per centimeter swum is the same for vertical migration as for maintaining a position in the water at night, the energy used in a round trip vertical migration of 100 m would be equivalent to that used to maintain a position for 10 h at night when the sinking speed was 0.28 cm/s. Thus, the difference between day and night sinking speeds would have to exceed 0.28 cm/s before a 100-m round trip could be considered an energy sparing mechanism. The difference in sinking rates exceeds 0.28 cm/s for larvae 13.5 mm and larger (Figure 6). This difference increases with larval length suggesting that the vertical range of migration over which energy savings are possible increases with length. In addition, the difference between day and night sinking speeds may be underestimated because sinking speeds were measured at the surface. If larvae descend during the day the gases in the swim bladder would be compressed, increasing body density and thereby increasing the sinking speed for larvae in the day.

These calculations are, of course, a great oversimplification, but they do illustrate that the energy saved by inflation of the swim bladder at night could exceed the cost of a vertical migration and that the possible range of migration could be greater for larger larvae.

The energy costs of maintaining a position in the water column for fish with and without swim bladders have been calculated by Alexander (1972). His calculations are not appropriate for anchovy larvae at night because he considered fish without a bladder to be continuously swimming and gaining lift from the pectoral fins. The behavior of an anchovy at night that failed to inflate the swim bladder would probably resemble one with an inflated bladder. It would sink motionless at an oblique angle to the water surface and interrupt sinking by bursts of near vertical swimming. To maintain a position, these bursts of swimming would have to be of longer duration or of greater frequency than if the swim bladder were filled.

In addition to an energy sparing mechanism, a nightly pattern of swim bladder inflation could possibly reduce predation. Some predators of larval fishes, for example chaetognaths and medusae, use the movement or turbulence produced by prey for detection and attack (Horridge 1966; Newbury 1972). Thus, the reduction of activity produced by slower sinking speeds could reduce predation. The vertical migration of the larvae could also result in exposure to different and possibly less hazardous predators at night. It would also serve to aggregate larvae, thus facilitating social contacts necessary for the development of schooling which begins at about 15 mm.

ACKNOWLEDGMENTS

Harold Dorr and Sharon Hendrix assisted in the laboratory work. James Zweifel provided statistical advice and Reuben Lasker and Paul Smith reviewed the manuscript. E. H. Ahlstrom allowed us to present original data on vertical distribution of anchovy larvae.

LITERATURE CITED

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.

ALEXANDER, R. McN.
1972. The energetics of vertical migration by fishes. Symp. Soc. Exp. Biol. 26:273-294.

BLAXTER, J. H. S., AND K. F. EHRLICH.
1974. Changes in behaviour during starvation of herring and plaice larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 575-588. Springer-Verlag, Berl.

BRAWN, V. M.
1962. Physical properties and hydrostatic function of the swim-bladder of herring (*Clupea harengus* L.) J. Fish. Res. Board Can. 19:635-656.

HORRIDGE, G. A.
1966. Some recently discovered underwater vibration receptors in invertebrates. *In* H. Barnes (editor), Some contemporary studies in marine science, p. 345-405. George Allen & Unwin Ltd., Lond.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.
In press. Behavior and survival of northern anchovy *Engraulis mordax* larvae. Symposium on Fishery Science Cienca Marinas, Spec. Suppl.

HUNTER, J. R., AND G. L. THOMAS.
1974. Effect of prey distribution and density on the searching and feeding behaviour of larval anchovy *Engraulis mordax* Girard. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 559-574. Springer-Verlag, N.Y.

IDA, H.
1972. Some ecological aspects of larval fishes in waters off central Japan. Bull. Jap. Soc. Sci. Fish. 38:981-994.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

MAIS, K. F.
1974. Pelagic fish surveys in the California Current. Calif. Dep. Fish Game, Fish Bull. 162, 79 p.

NEWBURY, T. K.
1972. Vibration perception by chaetognaths. Nature (Lond.) 236:459-460.

O'CONNELL, C. P.
1955. The gas bladder and its relation to the inner ear in *Sardinops caerulea* and *Engraulis mordax*. U.S. Fish Wildl. Serv., Fish. Bull. 56:505-533.

SCHOLANDER, P. F., L. VAN DAM, C. L. CLAFF, AND J. W. KANWISHER.
1955. Micro gasometric determination of dissolved oxygen and nitrogen. Biol. Bull. (Woods Hole) 109:328-334.

UCHIDA, K., S. IMAI, S. MITO, S. FUJITA, M. UENO, Y. SHŌJIMA, T. SENTA, M. TAHUKU, AND Y. DŌTU.
1958. Studies on the eggs, larvae and juveniles of Japanese fishes. [In Jap.] Kyushu Univ., Fac. Agric., Fish. Dep., 2d Lab. Fish. Biol., Ser. 1, 89 p.

UOTANI, I.
1973. Diurnal changes of gas bladder and behavior of postlarval anchovy and other related species. [In Jap., Engl. abstr.] Bull. Jap. Soc. Sci. Fish. 39:867-876.

WITTENBERG, J. B.
1958. The secretion of inert gas into the swim-bladder of fish. J. Gen. Physiol. 41:783-804.

CERIANTHARIA, ZOANTHIDEA, CORALLIMORPHARIA, AND ACTINIARIA FROM THE CONTINENTAL SHELF AND SLOPE OFF THE EASTERN COAST OF THE UNITED STATES

BERNT WIDERSTEN[1]

ABSTRACT

Specimens were examined from 95 stations located between lat. 37°49′N, long. 75°25′W and lat. 44°41′N, long. 66°14′W and from depths between 9 and 366 m. The material was collected by the Bureau of Commercial Fisheries, Biological Laboratory, Woods Hole, Mass., in the years 1955-68. The collection, which will be deposited in the Northeast Fisheries Center, National Marine Fisheries Service, Woods Hole, comprises two ceriantharian species, *Cerianthus borealis* and *Ceriantheopsis americanus*; one zoanthid species, *Epizoanthus incrustatus*; one species of *Corallimorpharia*, *Corynactis delawarei* n. sp., and 19 species of Actiniaria, *Edwardsia sulcata*, *Halcampa duodecimcirrata*, *Haloclava producta*, *Peachia parasitica*, *Bolcera tuediae*, *Tealia crassicornis*, *Actinostola callosa*, *Stomphia coccinea*, *Paranthus rapiformis*, *Antholoba perdix*, *Metridium senile fimbriatum*, *Haliplanella luciae*, *Sagartiogeton verrilli*, *Hormathia nodosa*, *Actinauge verrilli*, *Phelliactis americana* n. sp., *Amphianthus nitidus*, *Stephenauge nexilis*, and *Stephenauge* (?) *spongicola*.

The following description of the anthozoan species from the western North Atlantic is based on material collected by the Bureau of Commercial Fisheries, Biological Laboratory, Woods Hole, Mass., during 1955-68. The collection will be deposited in the Northeast Fisheries Center, National Marine Fisheries Service, Woods Hole.

Besides the morphological descriptions of different species, much importance has been attributed to the cnidom of the studied specimens. The sizes of the nematocyst capsules mentioned in the description refer to unexploded capsules.

While the fixation and preserving of the material in Formalin[2] and alcohol had only slightly affected the sizes of the nematocysts, the measurements of the column, tentacles, pedal disc, and other organs are, naturally, not directly comparable with those in living specimens.

The terminology used in this paper follows that by Stephenson (1935) and Carlgren (1949). The nomenclature of the nematocysts is the classical one, founded by Weill (1934) and amplified by Carlgren (1940a, 1945, 1949).

The sectioned mterial was stained with Heidenhain's azan or iron hematoxylin-eosin.

All nematocyst measurements are given in microns.

A list of the stations with names of the species collected at each station and with ADP (automatic data processing) codes for latitude and longitude; time, day, month, year, and number of collection; vessel; cruise; station number; gear; water depth; water temperature; and sediment type is on file at the Northeast Fisheries Center, Woods Hole.

DESCRIPTIONS

Ceriantharia
Cerianthidae

Cerianthus borealis Verrill 1873

OCCURRENCE.–40°10′N, 71°00′W, 146 m, silty sand, 1 specimen; 41°00′N, 70°48′W, ? m, 1 specimen; 41°50′N, 67°56′W, 51 m, sand, 2 specimens; 42°41′N, 70°05′W, 114 m, gravel, 2 specimens.

GENERAL CHARACTERISTICS.–The specimens were strongly damaged in their proximal parts. The morphology of the distal part of the body as well as the composition of the cnidom and the sizes of the nematocysts were typical of the species (cf. Carlgren 1940a). While the specimens from the two southernmost localities were young (diameter of the distal part of the body 4-8 mm), the other individuals were older, the largest of them being equipped with 150 labial as well as marginal tentacles.

[1]Institute of Zoology, Uppsala University, Uppsala, Sweden.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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FISHERY BULLETIN: VOL. 74, NO. 4, 1976.

NEMATOCYSTS (those of the southernmost specimen within parentheses).–*Marginal tentacles*: microbasic *b*-mastigophors 21 × 3.2-3.8 - 26 × 3.8, 36 × 4.4 - 41 × 4.9, 54.5 × 9.2 - 61 × 7.1 (25.3 × 3.8 - 28.3 × 4.4); atrichs 33 × 4.4 - 36 × 5.5 (9.8 × 1.6 - 27.5 × 2.7); spirocysts 20 × 3.3 - 56 × 6.5 (22 × 3.8 - 28 × 3.8-4.9). *Labial tentacles*: microbasic *b*-mastigophors (axial filament short and thin, less than half the length of the capsule) 37 × 3.8-4.4 - 45 × 5.5 (ca. 18.5 × 2.7); microbasic *b*-mastigophors (axial filament = about half the length of the capsule 20.7-35.4 × 3.8 (19.1 × 3.3 - 30.5 × 4.9); microbasic *b*-mastigophors (axial filament tall and coarse; more than half the length of the capsule) 57 × 8.3 - 63.7 × 7.1 (23.4-30 × 4.9-6); atrichs (not common) 55 × 9.8 - 63.7 × 28.3 (ca. 18 × 3.3); spirocysts 18 × 3.3 - 54 × 6 (14.7-16.8 × 2.7-3.3) μm. Holotrichs were very rare (in the distal part of the column = 22.3 × 14.7 - 43.6 × 17.4, and in the telocraspedon = 61 × 13.6 μm).

Ceriantheopsis americanus (Verrill 1864)

OCCURRENCE.–42°04′N, 67°30′W, 40 m, gravelly sand, 1 specimen; 42°25′N, 70°56′W, 13 m, 1 specimen.

GENERAL CHARACTERISTICS.–The proximal parts of the two studied specimens were missing. The individuals were young; the only specimen, being preserved with a 12-mm-long column part, had a diameter of 6 mm. The marginal tentacles were equipped with stout basal parts and acute apices. The labial tentacles were about 70 (69 in one specimen).

NEMATOCYSTS.–*Column* (distal part): microbasic *b*-mastigophors (not common) 19.6 × 3.8 - 32.7 × 5.5; atrichs (very common) 26 × 6.5 - 50 × 10.9-16.4. *Marginal tentacles*: microbasic *b*-mastigophors 16.3 × 3.8-4.4 - 19 × 4.9; atrichs (?) ca. 12 × 2.7, 8.7-12.5 × 4.9; spirocysts 12 × 2.7 - 27.3 × 4.9. *Labial tentacles*: microbasic *b*-mastigophors 16.3 × 3.8 - 32.7 × 6.5; spirocysts 13.6 × 2.7 - 27.3 × 4.9. *Actinopharynx*: microbasic *b*-mastigophors (axial filament more than half the length of the capsule) 21 × 4.9 - 32 × 6; microbasic *b*-mastigophors (axial filament less than half the length of the capsule) 13.6 × 2.7 - 18 × 3.3, 20.7 × 3.8 - 23 × 4.4. *Filaments* (orthocraspedon): microbasic *b*-mastigophors 19-21 × 3.3, 26 × 5.4 - 33 × 6.5; spirocysts (very rare) ca. 21 × 3.8 μm.

Zoanthidea
Epizoanthidae

Epizoanthus incrustatus Düben and Koren 1847

OCCURRENCE.–40°03′N, 71°16′W, 183 m, 4 specimens; 42°10′N, 65°37′W, 238 m, two colonies with 10 and 19 specimens respectively, and one solitary specimen, on a shell fragment.

GENERAL CHARACTERISTICS.–The color of the column and the coenenchyme is greyish brown; both are strongly encrusted with sand grains. The polyps were in the contracted state about 5 mm tall, with the column diameter about 4 mm. Most of the 17 capitular ridges as well as the insertions of the 36 mesenteries were indistinct (because it is heavily encrusted with sand). The tentacles numbered about 36.

NEMATOCYSTS.–*Column:* holotrichs 22 × 7 - 24 × 8.2; spirocysts 22 × 4.4 - 31 × 5.4. *Tentacles*: microbasic *p*-mastigophors 22-33 × 3.3 (35 × 6); microbasic *b*(?)-mastigophors 22-23.4 × 4.4; holotrichs 22-24 × 7.6-8.2 (common), 34 × 15.3 - 40 × 17.4 (not common); spirocysts (very common) 10 × 3.8 - 32 × 4.9. *Actinopharynx*: microbasic *p*-mastigophors (not common) ca. 22 × 6; holotrichs 21-25 × 7.6, 38 × 14.2 - 41 × 14.7. *Filaments*: microbasic *p*-mastigophors 20 × 5.4 - 28 × 6.5; microbasic *b*(?)-mastigophors 11 × 4.9 - 21 × 6; holotrichs 23 × 7.6 - 26 × 8.3 μm.

Corallimorpharia
Corallimorphidae

Corynactis delawarei n. sp.

HOLOTYPE.–Deposited as a series of sections in the Zoological Institute, Uppsala. Syntypes deposited in the U.S. National Museum, catalog number USNM 54322. Thirty-two specimens aggregated on a tube fragment of an onuphid polychaete, collected by the vessel *Delaware* from the type-locality on 14 June 1962, with a 1-m Naturalist dredge, in station number 9.

TYPE-LOCALITY.–39°56′N, 69°45′W, 201 m,

sandy bottom, on a tube fragment of an onuphid polychaete.

DIAGNOSIS.–Column rather firm, smooth, 15 mm tall, bright red (sometimes whitish) to reddish brown in color. Tentacles rather short, with well-limited acrospheres; two or three per endocoele, the total number being 90. Sphincter long, entodermal to ento-mesogloeal. Maximum number of mesenteries 60. At least six pairs of mesenteries perfect. Retractors diffuse. Cnidom: *column*–holotrichs and spirocysts; *tentacles* (acrospheres)–holotrichs and microbasic *b*- and *p*-mastigophors; *tentacles* (peduncles)– microbasic *b*- and *p*-mastigophors, atrichs (?), and spirocysts; *actinopharynx*–holotrichs, atrichs, microbasic *p*-mastigophors, and spirocysts; *filaments*–holotrichs, microbasic *p*-mastigophors, atrichs (?), and spirocysts.

GENERAL CHARACTERISTICS.–The column is smooth and rather firm. In the contracted state there are distally a number of transverse as well as a few longitudinal furrows. The shape of the column is proximally dependent on the shape of the substrate. The color of the column and the pedal disc is bright red to reddish brown. (There are also, however, some whitish individuals in the collection, with red mesenterial insertions shimmering through the ectoderm.) The longitudinal muscle sheet of the ectoderm forms a thin, but distinct layer in the column. The tentacles are rather short, with cylindrical peduncles and well-limited, white acrospheres. The entodermal as well as the ectodermal muscle sheets of the peduncles are well developed. The inner tentacles are shorter than the outer ones; the exocoelic tentacles are the largest. The stichodactyline arrangement of the tentacles is rather indistinct in the often strongly contracted specimens of the collection. There are, however, two or three tentacles per endocoele, the total number being 90. The sphincter is long, entodermal to entomesogloeal (Figure 1A), and is only occasionally capable of covering all the tentacles. The actinopharynx is short, in the contracted state, with longitudinal as well as transverse folds. There is only one indistinct siphonoglyph. The retractors of the maximum 60 mesenteries are diffuse, forming an insignificant sheet over the edge of the mesentery (Figure 1B). At least six pairs (including the directive pair) of the mesenteries are perfect. Reproduction is probably asexual by longitudinal fission. The size

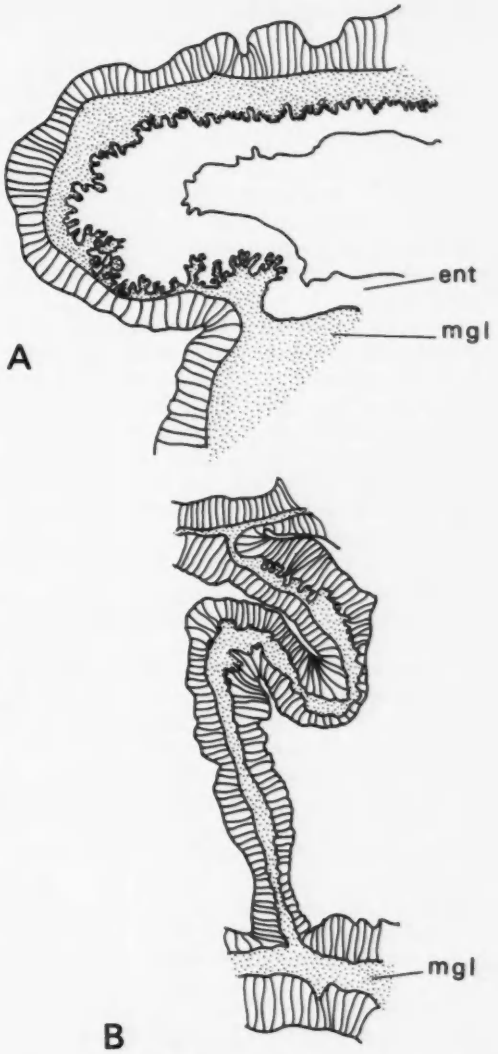


FIGURE 1.–*Corynactis delawarei* n. sp. A. Section through the sphincter region of the column. B. Cross section of a perfect mesentery. ent–entoderm, mgl–mesogloea.

of the normally cylindrical column is of a maximum 15 mm, with a proximal diameter of 8 mm.

NEMATOCYSTS.–*Column*: holotrichs 38 × 8.7 - 53.4 × 10.9; spirocysts 18.5 × 3.3 - 27 × 4.4. *Tentacles* (acrospheres): holotrichs 69 × 21.8 - 85 × 10.9-16.4; hoplotelous microbasic *p*-mastigophors 33 × 5.5 - 82 × 8.8-9.7; hoplotelous

microbasic *b*-mastigophors 31-34 × 4.4-4.9; 69-72 × 5.5 *Tentacles* (peduncles): microbasic *b*-mastigophors 19-24 × 3.8-4.9; microbasic *p*-mastigophors (very rare) ca. 36 × 7.6; atrichs (?) ca. 15 × 5.5; spirocysts 19 × 3.8 - 38 × 5.5. *Actinopharynx*: holotrichs 28 × 5.5 - 46 × 12; atrichs (rare) ca. 12 × 4.9; microbasic *p*-mastigophors (rare) ca. 22 × 6; spirocysts 17-23 × 3.8-4.4. *Filaments*: holotrichs 37 × 12 - 78 × 32.7; hoplotelous microbasic *p*-mastigophors 24 × 5.5 - 44 × 10.9-12; atrichs (?) 34 × 3.8-35 × 4.4; spirocysts (rare) ca. 31 × 3.8 μm.

The three individuals in the collection having a whitish color of the column (see above) deviate from the combination of the cnidom and the frequency of the nematocysts in some organs. *Tentacles* (acrospheres): holotrichs 49 × 16.4 - 65.4 × 35.4; atrichs (?) 22 × 5.5 - 41 × 10.4; microbasic *p*-mastigophors 19 × 4.9 - 46 × 6.5. *Tentacles* (peduncles): holotrichs ca. 66.5 × 19.6; hoplotelous microbasic *p*-mastigophors 37 × 7.1 - 64 × 8.7; microbasic *b*(?)-mastigophors 61 × 6.5 - 88 × 8.7; spirocysts 23 × 2.7 - 52 × 4.4 μm.

It is probable that the nematocysts characterized as atrichs in the tentacles of the whitish variety actually are holotrichs, the structure of which was made unobservable by the fixing agent. Difficulties in distinguishing between the two nematocyst types has been pointed out by Carlgren (1945) with concern to corallimorpharians.

Until studies on vital material of the whitish color form have been undertaken, which will possibly confirm the presence of atrichs in the acrospheres, I am inclined to consider it as a member of the species *Corynactis delawarei*. [In *Corynactis annulata* (Swedish Museum of Natural History, reference number 1244) collected off Tristan da Cunha, there is, however, a nematocyst equipment in the acrospheres suggestive of that described in the whitish color variety: holotrichs 46 × 12.5 - 60 × 9.3; microbasic *p*-mastigophors (rare) ca. 20 × 4.9; atrichs (?) 19 × 5.4 - 25 × 6.5 μm; microbasic *b*-mastigophors were not found in the specimen studied by me.]

Actiniaria
Edwardsiidae

Edwardsia sulcata (Verrill 1864)

OCCURRENCE.–44°00′N, 68°15′W, 110 m, silt-clay, 6 specimens, collected from three dredges.

GENERAL CHARACTERISTICS.–The physa is well developed. The scapus is divided into longitudinal compartments separated by the mesenterial insertions of the macrocnemes. The color of the scapus is yellowish grey. The nemathybomes are numerous and often closely aggregated (Figure 2A). The periderm is strong, but easily falls off; its color is yellowish brown. The scapulus is provided with high, longitudinally oriented ridges in the strongly contracted material. The maximum length of the scapus and scapulus is 40 mm, whilst the largest diameter is 4 mm. The 16 tentacles are conical, without ridges or nematocyst concentrations. The yellowish-white actinopharynx has one distinct siphonoglyph. The retractors of the eight macrocnemes are circumscribed and more or less reniform (Figure 2B). The parietal muscles are strongly developed with 10-12 partly branched muscle (lamellae on each side of the lamella of the septum (Figure 2C, D). The mesogloea of the mesentery is much thinner in the vicinity of the retractor portion than was described by Carlgren (1931) in *Edwardsia elegans* (Figure 2B).

NEMATOCYSTS.–*Scapus* (nemathybomes): microbasic *b*-mastigophors 90 × 5.4 - 110 × 6, 49 × 3.8 - 71 × 4.4 (the smaller nematocyst type has reached a considerable less degree of specialization than the larger type, the axial filament of which shows great conformity with that in *b*-mastigophors of *Edwardsia longicornis* Carlgren (cf. Carlgren 1940a). *Scapulus*: basitrichs 14 × 1.6 - 16 × 2.2. *Tentacles*: basitrichs 19-26 × 2.2-2.7; spirocysts 10 × 2.7 - 25 × 3.8. *Actinopharynx*: basitrichs 16-26 × 2.2; microbasic *p*-mastigophors (rare) ca. 24 × 4.4. *Filaments*: basitrichs 19 × 2.2 - 24 × 2.7; microbasic *p*-mastigophors (often with somewhat bent capsules; axial filament = one third to half the length of the capsule) 21-33 × 3.8-4.4; microbasic *p*-mastigophors (axial filament remarkably thin, and about three-fourths of the length of the capsule) 23-32 × 4.4-4.8 μm.

There are many morphological similarities between *E. sulcata* and *E. sipunculoides*. The *b*-mastigophors in the nemathybomes of the latter species are, however, always much smaller (in one specimen from the U.S. east coast, studied by me, they were 62 × 4.9 - 72.5 × 5.5, 42-44 × 4.4 μm; cf. also Carlgren 1931).

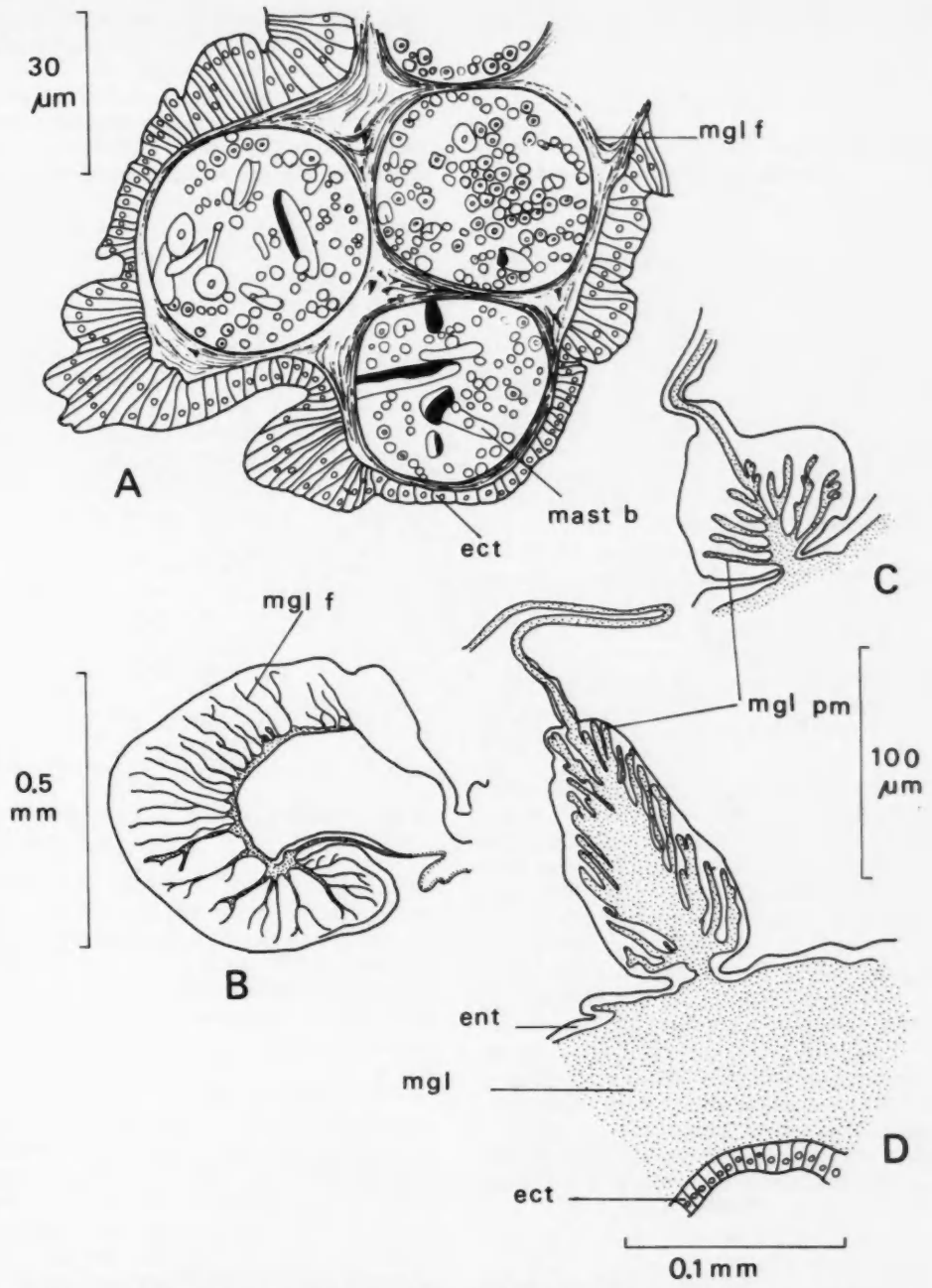


FIGURE 2.—*Edwardsia sulcata*. A. Section through three nemathybomes. B. Cross section through a retractor. C, D. Sections through two parietal muscles. ect—ectoderm, ent—entoderm, mast b—sectioned parts of microbasic *b*-mastigophors, mgl—mesogloea, mgl *f*—mesogloeal fibril, mgl pm—mesogloeal tract of parietal muscle.

Halcampa duodecimcirrata M. Sars 1851

OCCURRENCE.–43°10′N, 70°25′W, 64 m, till, 1 specimen.

GENERAL CHARACTERISTICS.–They agree with earlier descriptions of the species (cf. Carlgren 1893). The reddish scapus is provided with tenaculi and distinct mesenterial insertions shimmering through the ectoderm. The six pairs of macrocnemes (Figure 3A) (including two pairs of directives) have strongly developed, circumscribed, and reniform retractors (Figure 3B). The parietal muscles are provided with a rather small

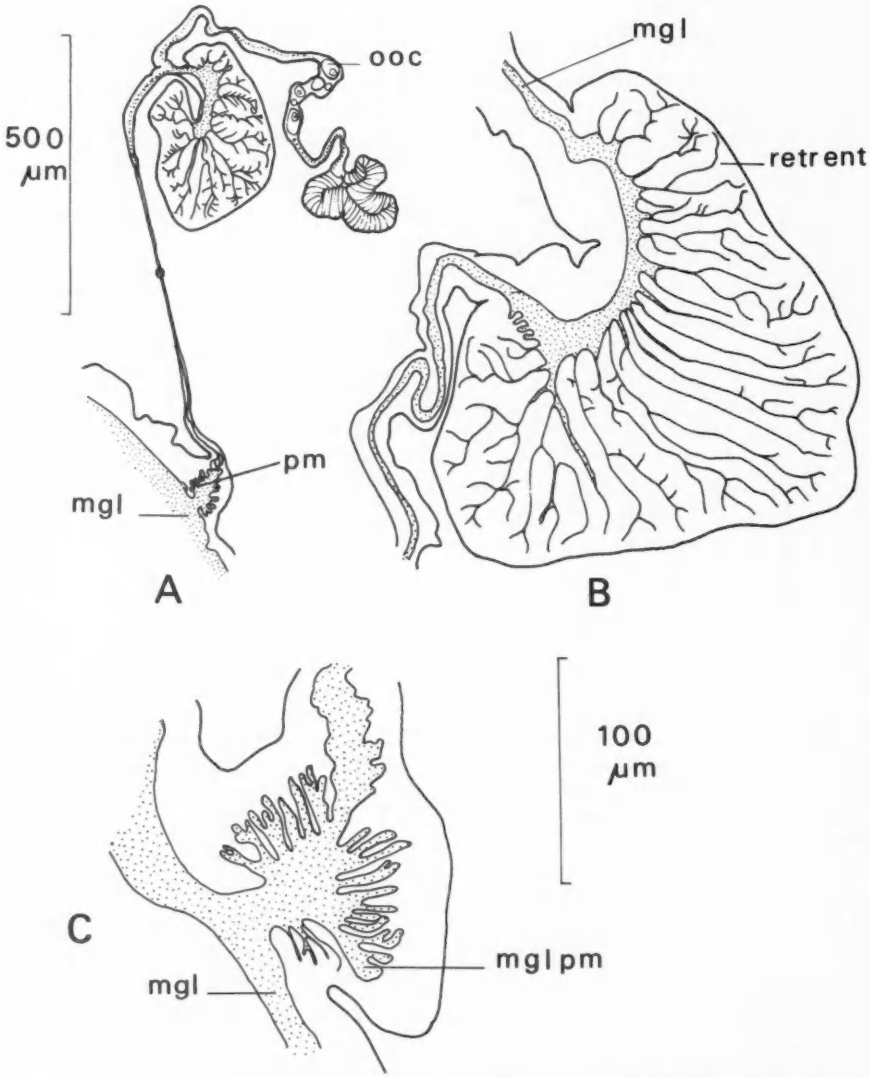


FIGURE 3.–*Halcampa duodecimcirrata*. A. Section through a macrocneme. B. Cross section of a retractor. C. Section through the peripheral part of a mesentery (the ectoderm is omitted in the figure). mgl–mesogloea, mgl pm–mesogloeal lamella of parietal muscle, ooc–oocyte, pm–parietal muscle, retr ent–entoderm of retractor muscle.

number of muscle lamellae (Figure 3C). The short, conical tentacles were 10 (12?) in number.

NEMATOCYSTS.–*Scapus*: basitrichs (rare) ca. 22 × 3.3, spirocysts (rare) ca. 28 × 3.8. *Scapulus*: spirocysts 25 × 3.8 - 49 × 4.4; basitrichs were not found in the very damaged scapular ectoderm. *Tentacles*: basitrichs (rare) 11.5 × 1.6-2.2 - 20 × 2.7; spirocysts 14 × 2.7 - 25 × 3.3. *Actinopharynx*: microbasic *p*-mastigophors 24-32 × 3.5; spirocysts 17 × 2.2 - 25 × 4.9. *Filaments*: microbasic *p*-mastigophors 22-23 × 4.4-4.9; basitrichs (?) 12-13.6 × 3.8 μm.

The alleged differences as to the form of the tentacles between *H. duodecimcirrata* and *H. chrysanthellum* would argue against my decision to refer the specimen to the former species. Considering the extensive contraction of the specimen, this characteristic must, however, be regarded as of minor importance. Of greater importance here is the conformity with *H. duodecimcirrata* of the sizes of the nematocysts in different organs (cf. Carlgren 1940a). The number of fertile mesenteries (eight in the studied specimen) is another argument for the individual being placed in *H. duodecimcirrata*.

Haloclavidae

Haloclava producta (Stimpson 1856)

OCCURRENCE.–39°00′N, 74°45′W, 15 m, sandy bottom, 1 specimen.

GENERAL CHARACTERISTICS.–The column of the strongly contracted and partly damaged specimen is fusiform with the ectoderm in closely lying, transverse folds. The color is grey. The scapus has a few sand grains attached to the ectoderm. The length of the column is 16 mm, with the greatest diameter (at the middle of the body) about 8 mm. The retractors of the protomesenteries are very strong, circumscribed, and reniform (Figure 4A). The four pairs of metamesenteries are weaker than the protomesenteries. The parietal muscles are rather strong (Figure 4B). There is no sphincter. The actinopharynx is rather short with a very deep siphonoglyph. The number of tentacles was impossible to confirm; as there were only mesogloeal fragments left of the tentacles, neither the nematocyst types nor their sizes can be treated. The location of the fragments of the tentacles favors the belief that there are 20 tentacles in the living animal.

NEMATOCYSTS.–*Column*: basitrichs 20 × 2.7 - 24.5 × 3.3. *Actinopharynx*: basitrichs 14 × 2.2 - 17.4 × 2.7, 38-57 × 4.4-4.9; spirocysts (only one found) 43.1 × 3.8. *Filaments*: basitrichs 14 × 2.7 - 25 × 3.3, 70-83 × 4.4-5.5, 54.5 × 7 - 75 × 6.5-7.1 μm.

Peachia parasitica (Agassiz 1859)

OCCURRENCE.–44°16′N, 67°38′W, 91 m, silt-clay, 1 specimen.

GENERAL CHARACTERISTICS.–The column of the specimen is strongly contracted, with the length 24 mm and the largest diameter (at the middle of the body) 15 mm. The proximal diameter of the column is 8 mm. The exact arrangement of the extended lobes of the conchula was not possible to observe in the specimen. There is no sphincter. The only siphonoglyph is thick-walled and of the typical *Peachia* appearance. The number of mesenteries are 20, six pairs being perfect, and supplied with strong, diffuse retractors with rather high muscle lamellae. The four pairs of imperfect mesenteries are equipped with rather small, diffuse retractors and are laterally and ventrolaterally located. The 10 conical tentacles have broad bases.

NEMATOCYSTS.–*Column*: basitrichs 27-34 × 3.8-4.4. *Tentacles*: basitrichs 27-39 × 3.8-4.4; spirocysts ca. 23 × 3.3 *Actinopharynx*: basitrichs 40-46 × 5.5; spirocysts 19-23 × 2.2-2.7. *Filaments*: basitrichs 27 × 3.8 - 38 × 4.4; basitrichs (?) 39 × 6 - 45 × 7.6; microbasic *p*-mastigophors (rare) ca. 28 × 3.8 μm.

The filamental nematocysts named "basitrichs (?)" (above) might be *p*-mastigophors. As I have had no chance of observing the exploded capsules and as the axial filament does not show the typical *p*-mastigophor structure in the unexploded capsules, I am not now inclined to consider these nematocysts, which are probably homologous to the "penicilli-like mastigophors" found by Carlgren (1940b), as microbasic *p*-mastigophors.

Actiniidae

Bolocera tuediae (Johnston 1832)

OCCURRENCE.–41°27′N, 69°02′W, 146 m, 1 specimen; 41°50′N, 69°26′W, 165 m, 1 specimen; 42°15.5′N, 69°59.5′W, ? m, 1 specimen; 42°25′N,

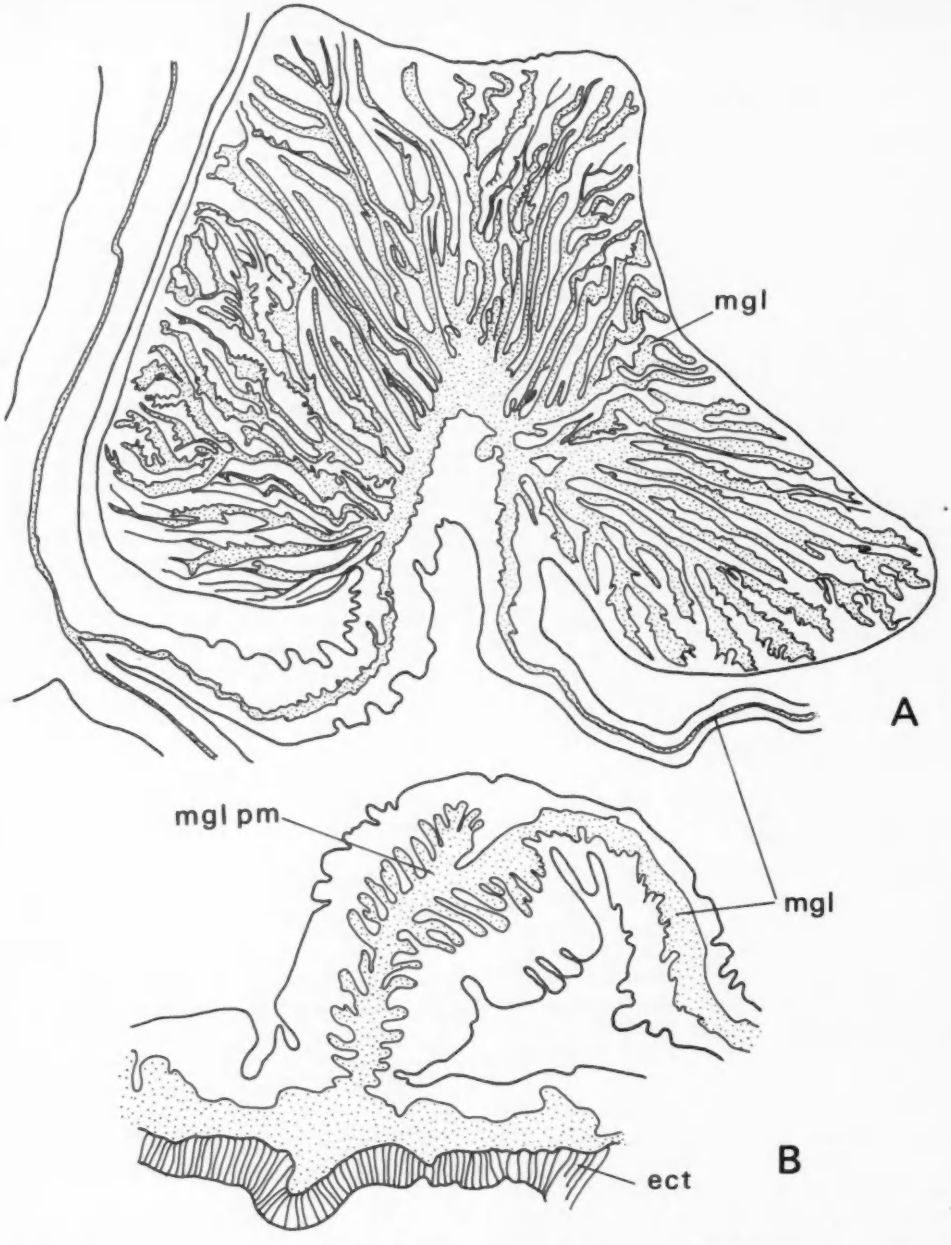


FIGURE 4.—*Haloclava producta*. A. Section through a retractor muscle. B. Section through the peripheral part of a mesentery and adjacent parts of the body wall. ect—ectoderm, mgl—mesogloea, mgl pm—mesogloeal tract of parietal muscle.

67°06′W, 366 m, 3 specimens; 42°48′N, 69°39′W, 183 m, 1 specimen; 43°17′N, 70°24′W, 46 m, 1 specimen; 43°19′N, 67°16′W, 201 m, 1 specimen; 43°20′N, 68°45′W, 119 m, 1 specimen.

GENERAL CHARACTERISTICS.–The structure of the specimens agrees with earlier descriptions of the species (cf. Carlgren 1891:242, 1893:50; Stephenson 1935:130; Verrill 1922:G 115).

NEMATOCYSTS.–*Column*: basitrichs 16 × 2.2 - 21 × 2.7, 33 × 3.3 - 41 × 3.8 (-63 × 5.5). *Tentacles*: basitrichs 21 × 2.7 - 36.5 × 3.3-3.8, 52 × 3.8 - 87 × 4.9-6.5 (most often 60-70 × 4.5-6); spirocysts 31-74 × 3.3-5.5; *Actinopharynx*: basitrichs 50 × 4.4 - 79 × 5.5; microbasic *p*-mastigophors 23-33 × 5.5 *Filaments*: basitrichs 20-22 × 2.7-3.8, 50 × 3.8 - 74 × 4.4-5.5; microbasic *p*-mastigophors 19.6 × 4.9 - 35.4 × 5.5 μm.

Tealia crassicornis (Müller 1776)

OCCURRENCE.–41°02′N, 69°00′W, 80 m, gravelly sand, 1 specimen; 41°13′N, 68°58′W, 102 m, gravelly sand, 3 specimens; 41°33′N, 69°47′W, 27 m, gravelly sand, 1 specimen; 41°50′N, 67°56′W, 51 m, sand, 3 specimens; 42°11′N, 65°56′W, 229 m, gravel, 1 specimen; 42°25′N, 66°05′W, 249 m, gravel, 1 specimen; 42°26′N, 67°02′W, 366 m, 2 specimens; 43°11′N, 66°31′W, 92 m, gravel, 3 specimens; 43°11′N, 67°05′W, 181 m, 1 specimen; 43°12′N, 65°33′W, 73 m, shelly sand, 1 specimen; 43°33′N, 69°35′W, 159 m, 1 specimen; 43°37′N, 68°12′W, 198 m, 1 specimen; 43°49′N, 68°31′W, 95 m, 2 specimens; 43°52′N, 66°42′W, 102 m, 2 specimens; 43°53′N, 68°38′W, 91 m, 1 specimen; 44°26′N, 67°28′W, 73 m, till, 1 specimen; 44°30′N, 66°30′W, 157 m, 1 specimen.

GENERAL CHARACTERISTICS.–The morphology of the studied specimens agrees with earlier descriptions of the species (cf. Verrill 1867; Carlgren 1893). The pedal disc is wide, circular (diameter = 16-114 mm) or oval (16 × 22 - 47 × 63 mm). The rather firm column is in the contracted state, cylindrical to semispherical, 14-38 mm high. In those cases where the column is provided with verrucae, these are chiefly spread over the distal parts of the column. In some specimens there is a distinct annulus with 48 marginal verrucae. The number of mesenteries is somewhat larger proximally than distally (in a specimen with 68 mesenteries only four were limited to the proximal part of the column). The two outer of the four to five mesenterial cycles are often not quite completed. With the exception of the youngest, proximally located cycle, and the 10 oldest perfect pairs, the mesenteries are fertile. In the specimens coming from 43°11′N, 66°31′W, the entodermal and circumscribed sphincter is obviously asymmetric, with one half of it considerably more strongly developed than the other.

Many of the specimens in the collection are viviparous with larvae and young stages equipped with tentacles lying in the proximal part of the gastrocoele.

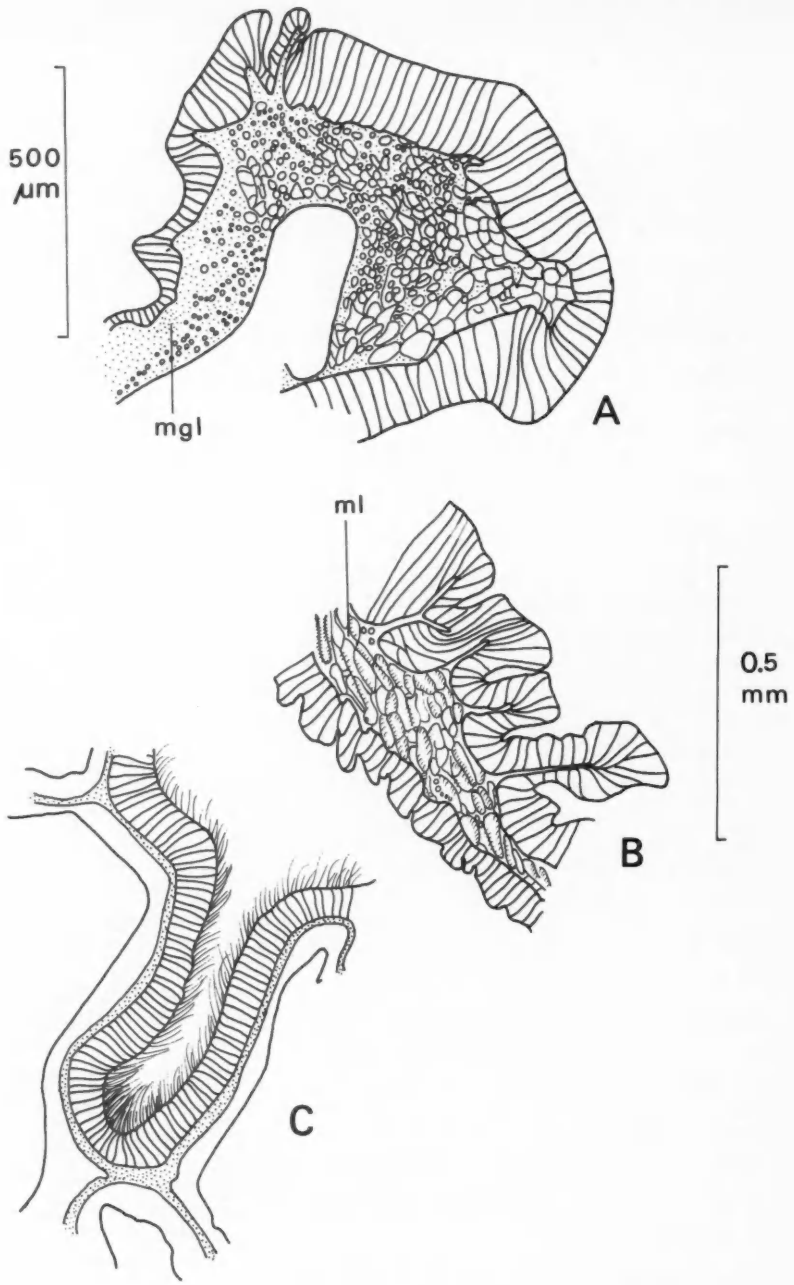
NEMATOCYSTS.–*Column*: basitrichs 5.5 × 1.1 - 9 × 2.7, 18 × 2.2 - 27 × 2.7-3.3; in larger specimens found in the deeper localities: 12.5-14 × 2.7, 23-37 × 3.8, 79 × 5.5 - 83.4 × 8.2; spirocysts 22 × 2.7 - 69 × 4.4. *Tentacles*: basitrichs 10-14 × 2.2-2.7, 20 × 1.6 - 36.5 × 2.7-3.8; spirocysts 17.4 × 2.7 - 71 × 4.9-5.5. *Actinopharynx*: basitrichs 49 × 5.5-6 - 91 × 6-7.1, 12 × 1.6 - 26 × 2.7; microbasic *p*-mastigophors 23 × 4.9 - 30 × 5.5-6.5; spirocysts (rare) 28-41 × 3.8. *Filaments*: basitrichs 11 × 2.2 - 34 × 2.7, 49 × 5.5-6 - 68 × 7.1; microbasic *p*-mastigophors 20 × 4.9 - 41 × 6.5 μm.

Actinostolidae

Actinostola callosa (Verrill 1882)

OCCURRENCE.–42°10′N, 69°57′W, 142 m, 1 specimen; 42°11′N, 68°16′W, 198 m, 1 specimen; 42°21′N, 68°02′W, 190 m, 3 specimens; 42°26′N, 66°35′W, 302 m, 1 specimen; 42°27′N, 66°08′W, 247 m, gravel, 1 specimen; 42°51′N, 65°12′W, 159 m, 1 specimen; 42°54′N, 69°35′W, 159 m, 2 specimens; 43°21′N, 69°57′W, 155 m, 1 specimen; 44°41′N, 66°14′W, 134 m, till, 1 specimen.

GENERAL CHARACTERISTICS.–The morphology of this species has been carefully described by Carlgren (1893:71). The length of the column varies between 13 and 196 mm, and the diameter of the pedal disc is 13-48 mm. The tentacles are arranged in six cycles (6+6+12+24+48+96). The mesenteries (in five or six cycles) are arranged according to the *Actinostola* rule. Twenty-four pairs of mesenteries are perfect, those of the two inner cycles (including the two directive pairs) being sterile, as well as those of the outer cycle.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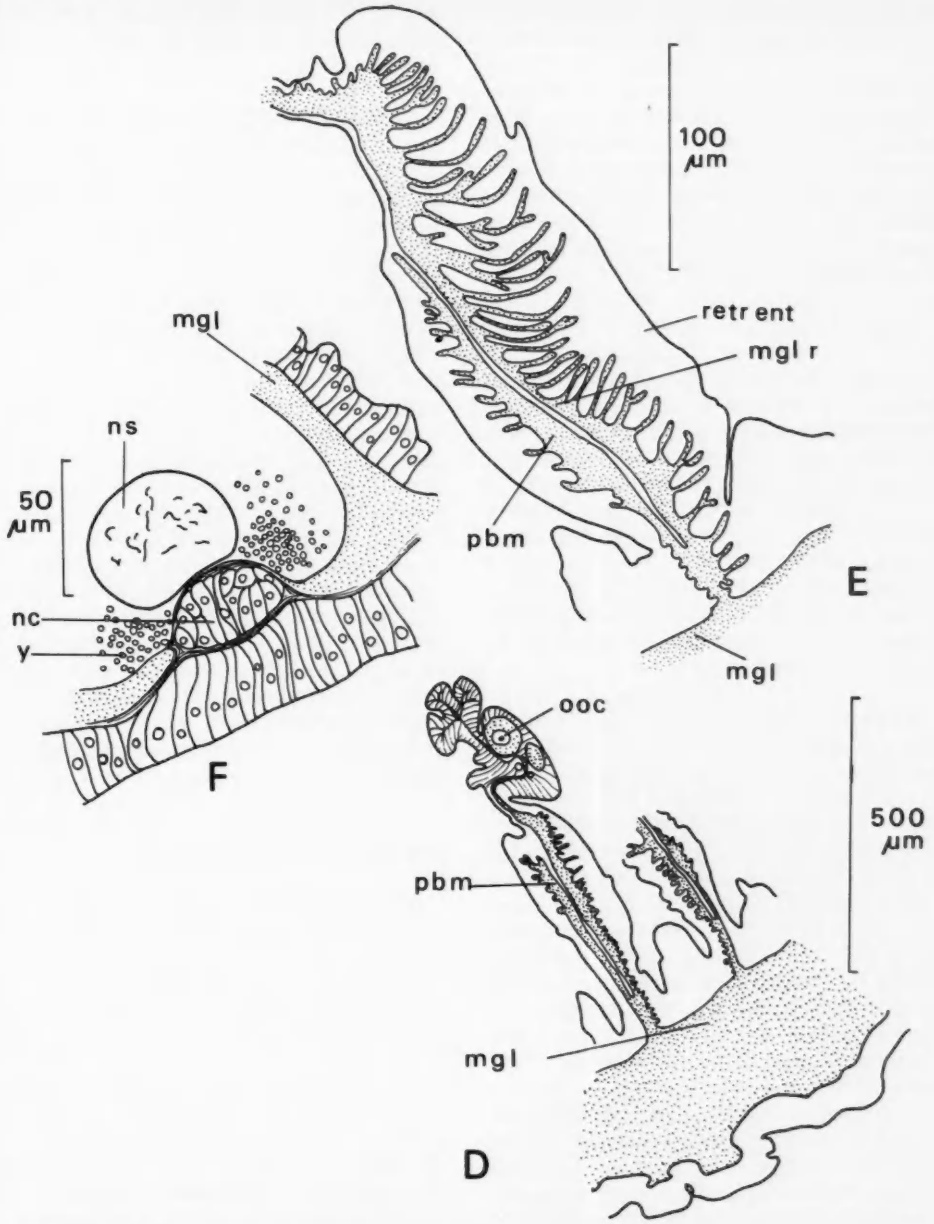


FIGURE 5.—*Stomphia coccinea*. A. Cross section of the sphincter in a young specimen. B. Section through part of a tentacle showing the arrangement of the muscle fibrils (ml) in a young specimen. C. Section through a siphonoglyph. D. Section through a mesentery in a young specimen. E. Section through a retractor and parietobasilar muscle of a young specimen. F. Section of an oocyte and nurse cells. mgl—mesogloea, mgl r—mesogloea of retractor, nc—nurse cell, ns—nucleus, ooc—oocyte, pbm—parietobasilar muscle, retr ent—entoderm of retractor muscle, y—yolk.

NEMATOCYSTS.–*Column*: basitrichs 19 × 2.7 - 35.4 × 2.7-3.3; spirocysts 24.5 × 3.3 - 57 × 5.5-6. *Tentacles*: basitrichs 26 × 2.2 - 41 × 2.7 (most often 30-35 × 2.7); microbasic *b*-mastigophors (in the apex) 42.5 × 7.1 - 56 × 7.1-8.2; spirocysts 27 × 2.7 - 64 × 7.6. *Actinopharynx*: basitrichs 21-32 × 2.7; microbasic *p*-mastigophors 22-28 × 4.9. *Filaments*: microbasic *p*-mastigophors 21-28 × 4.4, 20-29 × 5.5 μm. The cnidom in specimens from the eastern North Atlantic was described by Carlgren (1940a).

Stomphia coccinea **(Müller 1776)**

OCCURRENCE.–41°20′N, 69°22′W, 49 m, 3 specimens; 41°37′N, 66°16′W, 91 m, sand, 4 specimens; 42°18′N, 65°28′W, 113 m, sandy gravel, 1 specimen; 42°32′N, 65°39′W, 95 m, gravel, 1 specimen; 42°40′N, 65°56′W, 91 m, sandy gravel, 4 specimens; 43°10′N, 66°04′W, 92 m, gravel, 1 specimen; 43°21′N, 66°22′W, 60 m, shelly gravel, 2 specimens; 44°12′N, 66°36′W, 91 m, gravel, 1 specimen; 44°16′N, 66°28′W, 201 m, gravel, 1 specimen; 44°24′N, 67°14′W, 90 m, till, 1 specimen; 44°25′N, 66°25′W, 188 m, till, 3 specimens; 44°26′N, 66°19′W, 174 m, till, 1 specimen.

GENERAL CHARACTERISTICS.–The morphology of the studied specimens agrees with earlier descriptions made of the species (e.g., Carlgren 1893). The height of the contracted column is 3-28 mm. The pedal disc is wide with a distinct limbus. The relations between the length of the column and the diameter of the pedal disc is in the contracted state 14/23-7/17. The mesogloeal, diffuse sphincter is distally very strong (Figure 5A). The tentacles, conical and longitudinally furrowed with an apical pore, are arranged in four (sometimes five ?) cycles. The tentacular muscles are mesogloeal (Figure 5B). The number of mesenteries varies (in one of the larger specimens it is equal to 120 in the proximal part of the body). Most often (with the exception of the southernmost specimens) there are 16 pairs of perfect and sterile mesenteries. (In the specimens from 41°20′N, the number of perfect and sterile mesenteries is approximately 24-29, with an organization reminiscent of that in, e.g., *Parasicyonis*.) The long, folded actinopharynx is equipped with two siphonoglyphs (Figure 5C). All the imperfect mesenteries excluding those of the last cycle are often fertile (Figure 5D), the oocytes being provided with well-developed nurse cells (Figure 5F) during oogenesis. The parietobasilar muscles form even in very young individuals their own lobes high up in the column (Figure 5D, E).

NEMATOCYSTS.–*Column*: basitrichs 12-20 × 2.2-2.7, 30.5-38 × 4.4-5.5. *Tentacles*: basitrichs 14 × 2.2 - 24.5 × 3.3; microbasic *b*-mastigophors (30.5 × 6.5 -) 39-53 × 6.5-7.1; spirocysts 19 × 3.3 - 50 × 4.4-5.5 (in the young specimen from 44°24′N, the column of which was 3 mm high and the number of tentacles equal to 36, there was a somewhat different size for the tentacular nematocysts: basitrichs 15 × 2.2 - 22 × 2.7, microbasic *b*-mastigophors 28 × 5.3 - 33 × 7.1, spirocysts 14-22 × 2.7-3.8 μm). *Actinopharynx*: basitrichs 14 × 2.2 - 23 × 3.8; microbasic *p*-mastigophors 18 × 3.3 - 27 × 4.9; spirocysts 22 × 3.8 - 57 × 4.9-5.5. *Filaments*: basitrichs 9.5 × 2.2 - 22 × 2.7; microbasic *p*-mastigophors (17 × 3.8 -) 19 × 4.9 - 29 × 5.5, 24 × 3.3 - 29 × 3.3-4.4 μm.

My placing of the three specimens from the southernmost station within *S. coccinea* may be discussed. In some morphological characteristics, they resemble *Anthosactis* as well as *Parasicyonis*; apart from the development of the perfect mesenteries, the morphological differences between these, obviously young individuals, and the adult, typical *S. coccinea* are, however, not so comprehensive as to require description of a new subspecies.

Paranthus rapiformis **(Lesueur 1817)**

OCCURRENCE.–37°49′N, 75°25′W, 12 m, sand-silt-clay, 1 specimen.

GENERAL CHARACTERISTICS.–The column is smooth, much wider distally than proximally, and with a reddish brown color. The length of the column is 26 mm, with the proximal diameter 8 mm; the distal is 23 mm. The numerous tentacles are arranged in five (six ?) cycles. They are imperfectly retractile and acuminate. The sphincter is mesogloeal, of diffuse type, and weak. The yellowish, longitudinally folded actinopharynx is provided with two siphonoglyphs. The mesenteries are proximally fewer than distally, where they are arranged in four cycles (6+6+12+24 pairs). Twelve pairs of mesenteries (including the two pairs of directives) are perfect. The mesenterial retractors are of diffuse-restricted type. The parietobasilar muscles are only

slightly developed. The pedal disc is well defined and excavated. The individual studied was sterile.

NEMATOCYSTS.–*Column* (distally): basitrichs 17 × 1.6; microbasic *p*-mastigophors (?) ca. 16 × 3.3; spirocysts 33-60 × 3.8. *Column* (proximally): basitrichs 21-26 × 2.2, 16 × 2.7 - 26 × 3.8; microbasic *p*-mastigophors (rare) ca. 33 × 5.5; spirocysts 14 × 2.7 - 53 × 3.3. *Tentacles:* basitrichs 22 × 2.2 - 24.5 × 2.7; microbasic *p*-mastigophors 22 × 3.8 - 27 × 4.4; spirocysts 15 × 2.2 - 26 × 3.3. *Actinopharynx*: basitrichs 25 × 2.7 - 30 × 3.3; microbasic *p*-mastigophors 18.5 × 4.9 - 24.5 × 6; microbasic *p*(?)-mastigophors 27 × 4.9 - 30 × 5.5. *Filaments*: basitrichs 22 × 3.3 - 32 × 3.8-4.9; microbasic *p*-mastigophors (axial filament = about half the length of the capsule) 20 × 4.4 - 26 × 5.4; microbasic *p*-mastigophors (axial filament = almost the length of the capsule) 12.5 × 4.4 - 15 × 4.9; spirocysts 49-57 × 3.8-5.5 μm.

The most obvious difference between the above-mentioned specimen and the earlier description of the species (cf. Carlgren and Hedgpeth 1952:159), besides the different color of the column and the occurrence of 12 pairs of perfect mesenteries, is the size of the filamental basitrichs. While the filaments in material from Port Aransas and Port Isabel are provided with basitrichs ranging in size from 12.7 to 14 × 2.2 μm, the above-described specimen has much larger nematocysts of the corresponding type: 22 × 3.3 - 32 × 4.9 μm. The same tendency can be seen also with regards to the basitrichs of the column.

Antholoba perdix **(Verrill 1882)**

OCCURRENCE.–40°06′N, 71°00′W, 179 m, 1 specimen; 40°10′N, 70°00′W, 114 m, silty sand, 1 specimen; 40°10′N, 71°15′W, 110 m, silty sand, 1 specimen.

GENERAL CHARACTERISTICS.–The column is smooth and, in the material studied, transversely wrinkled. The smaller specimens are olive-shaped; the larger specimen is cup-shaped with an expanded distal part. The color is greyish, with scattered, irregularly shaped, brownish spots. The oral disc of the larger specimen is greyish yellow with faintly marked, brown, and radially directed streaks. An outer lip-shaped fold is here provided on its outside with a zone, reddish brown in color. Two parallel ribbons of the same color divide this fold and the central part of the oral disc into two halves. The excavated pedal disc is faintly set off from the column. The length of the column is 12-21 mm, and its diameter is 16-44 mm. The pedal disc is maximally 23 mm in diameter. The tentacles are numerous (in the largest specimen about 600), short and conical, greyish in color. They are longitudinally furrowed and provided with an apical pore; in the smaller specimens they are sometimes equipped with small, papillar processes. The tentacles are arranged in five cycles, those of the outer cycles being much smaller than the inner ones (even in the largest specimen the outer tentacles are papillary). The fifth cycle of mesenteries is not complete. The number of perfect mesenteries in the larger specimen is 48. There are more mesenteries distally than proximally. The sphincter is alveolar (Figure 6). The retractors are diffuse and extended in length. The entoderm of the tentacles and the oral disc is reddish brown. All the specimens were sterile.

NEMATOCYSTS.–*Column*: basitrichs 20-28 × 2.7-3.3. *Tentacles*: basitrichs 15-16 × 1.6-2.2, 23 × 2.2 - 36 × 3.3-3.8; spirocysts (very numerous)

FIGURE 6.–*Antholoba perdix*. Sections through the distal parts of the sphincter in young specimens. mgl–mesogloeal layer.

19 × 3.3 - 46 × 3.8. *Actinopharynx*: basitrichs 14 × 1.6 - 16 × 2.2 (- 27 × 2.7); microbasic *p*-mastigophors 15 × 3.3 - 31 × 4.9. *Filaments*: basitrichs 14 × 1.6 - 28 × 2.7; microbasic *p*-mastigophors (very numerous) 14 × 4.4 - 31× 4.9-5.5 μm.

Metridiidae

Metridium senile fimbriatum (Verrill 1865)

OCCURRENCE.–40°35′N, 67°59′W, 84 m, gravel, 5 specimens; 40°40′N, 68°01′W, 84 m, sand, 1 specimen; 40°51′N, 68°55′W, 66 m, sand, 4 specimens; 41°04′N, 71°24′W, 42 m, 1 specimen; 42°00′N, 69°56′W, 48 m, gravelly sand, 1 specimen; 42°15′N, 70°12′W, 26 m, 3 specimens; 42°22′N, 70°18′W, 33 m, 2 specimens; 42°42′N, 65°18′W, 91 m, 1 specimen; 42°42′N, 65°40′W, 90 m, 3 specimens; 42°47′N, 66°25′W, 99 m, 1 specimen; 42°54′N, 66°14′W, 166 m, 2 specimens; 43°07′N, 65°57′W, 97 m, 1 specimen; 43°17′N, 65°35′W, 40 m, gravel, 1 specimen; 43°36′N, 68°50′W, 115 m, 2 specimens; 43°43′N, 66°30′W, 84 m, 1 specimen; 43°44′N, 66°28′W, 75 m, 1 specimen.

GENERAL CHARACTERISTICS.–They agree with earlier descriptions of the species (cf., e.g., Carlgren 1893:102). The height of the column varies between 5 and 35 mm, and the diameter of the pedal disc is 7-47 mm. The color is yellow to yellowish brown in the preserved state. The specimens from 40°51′N were all very young, the youngest being equipped with only 12 tentacles.

NEMATOCYSTS (sizes of the above-mentioned, small specimens in parentheses).–*Column*: basitrichs 15 × 2.7 - 19 × 3.3 (10 × 1.6 - 12 × 2.2); microbasic amastigophors 26-28 × 3.8-4.4 (16 × 3.3 - 21 × 3.8-4.4); microbasic *p*(?)-mastigophors 23-31 × 3.8-4.4; spirocysts 22-27 × 3.3-3.8. *Tentacles*: basitrichs (11.5 × 1.6 -) 18 × 2.2 - 28 × 2.7-3.3 (17-21 × 2.7-3.3); microbasic amastigophors 13 × 2.7 - 15 × 3.3; spirocysts 21 × 3.3 - 31 × 4.9 (11 × 2.7 - 17 × 4.4). *Actinopharynx*: basitrichs 26-39 × 3.8 (17 × 2.2 - 27 × 2.7-3.3); microbasic *p*-mastigophors 22-23 × 3.8 (17-23 × 3.3-3.8); microbasic amastigophors (rare) ca. 31 × 4.4. *Filaments*: basitrichs (very rare) ca. 14 × 3.8 (12 × 2.7); microbasic *p*-mastigophors 16-25 × 4.4, 24-32 × 3.8-4.4 (12-14 × 4.4, 21-23 × 3.8-4.4). *Acontia*: microbasic *b*-mastigophors 51-67 × 3.2-4.9 (40 × 3.8 - 57 × 4.4); microbasic amastigophors (28 × 3.8 -) 49-64 × 4.9-5.5 (36 × 4.4 - 55 × 5.5) μm.

Aiptasiomorphidae

Haliplanella luciae (Verrill 1898)

OCCURRENCE.–39°00′N, 76°22′W, 16 m, silty clay, 10 specimens.

GENERAL CHARACTERISTICS.–They agree with earlier descriptions (Stephenson 1925:888, 1935:197; Field 1949:10). The sizes of the nematocyst capsules deviate, however, in some respects from what has been described earlier (cf. Carlgren 1940a).

NEMATOCYSTS.–*Column*: basitrichs 10-11 × 1.6, 19 × 3.3 - 23 × 3.8; microbasic *p*- or amastigophors 19 × 3.8 - 21 × 4.4. *Tentacles*: basitrichs 15 × 1.6 - 20 × 2.2; microbasic *p*-mastigophors 18 × 3.8 - 25 × 4.9; spirocysts ca. 16 × 4.4-4.9. *Actinopharynx*: basitrichs (?) (the capsules are slightly bent) 30-32 × 2.7-3.3; microbasic *p*-mastigophors 23-27 × 3.8; microbasic *p*- or amastigophors 21-23 × 2.7-3.3. *Filaments*: basitrichs 14 × 1.6 - 19 × 2.2; microbasic *p*-mastigophors 22-28 × 3.8; microbasic a(?)-mastigophors 17 × 3.3 - 28 × 3.8; spirocysts 12.5 × 2.7 - 17 × 5.4. *Acontia*: basitrichs 15-18 × 1.6; microbasic *p*-mastigophors 43 × 5.5 - 56 × 6.5 μm. It was not possible to determine if there are any microbasic amastigophors present in the acontia, as all the mastigophor capsules were unexploded.

The only difference in the cnidom of the above-mentioned specimens and earlier descriptions of the species (cf. Carlgren 1945; Field 1949) besides the unsettled presence of microbasic amastigophors in the acontia (cf. Hand 1955) are the occurrence in this sample, of basitrichs in the actinopharynx, in agreement with the conditions in *Aiptasiomorpha texaensis* (cf. Carlgren and Hedgpeth 1952).

Sagartiidae

Sagartiogeton verrilli Carlgren 1942

OCCURRENCE.–40°32′N, 67°05′W, 338 m, 3 specimens, on fragments of mussel shell; 42°25′N, 66°21′W, 256 m, gravel, 1 specimen.

GENERAL CHARACTERISTICS.–The length

of the column varies between 8 and 18 mm, whilst the diameter of the pedal disc is 12-20 mm. The column is greyish, salmon-colored and divisible into scapus and scapulus. The scapus is provided with distinct mesenterial insertions shimmering through the ectoderm and has small tenaculi. The tentacles of the studied specimens are about 9 mm long, conical and acute. They are hexamerously arranged; in the largest specimen there are five cycles (6+6+12+24+40). The reddish-brown actinopharynx is strongly folded and provided with two siphonoglyphs. The color of the tentacles is greyish white, the largest specimen with reddish-brown pigmentation. The pairs of mesenteries are arranged in four to five cycles (proximally there are 90-100 mesenteries–distally only half the number are developed). The number of perfect mesenteries tends to vary. In one of the studied specimens there are 17 pairs (including the two directive pairs). The first cycle of mesenteries is sterile. The retractors of the first cycle of mesenteries are strong, of a circumscribed diffuse type (Figure 7A); in the other mesenteries they are diffuse. The parietobasilar muscles are rather weak (Figure 7B). The acontia are numerous and whitish in color. The mesogloeal, diffuse spincter is rather long.

NEMATOCYSTS.–*Scapus*: basitrichs 9-11.5 × 1.6, 16-17 × 2.2-3.3; microbasic amastigophors 30.5-35 × 4.4, ca. 15 × 3.8 (rare). *Tentacles*: basitrichs 13 × 2.2 - 27 × 2.7; microbasic amastigophors (16 × 3.8 -) 26 × 4.4 - 44 × 6.5; spirocysts 22 × 3.8 - 36 × 6. *Actinopharynx*: basitrichs 27-32 × 3.3; microbasic *p*-mastigophors ca. 23 × 4.4, 27-31 × 4.4-4.9. *Filaments*: basitrichs (rare) ca. 27 × 3.8; microbasic *p*-mastigophors 26-31 × 4.4-4.9; spirocysts 22 × 4.9 - 34 × 6. *Acontia*: basitrichs 36.5 × 3.8 - 43 × 4.4-4.9; microbasic amastigophors 57 × 6 - 64 × 7.1 μm.

Hormathiidae

Hormathia nodosa (Fabricius 1780)

OCCURRENCE.–40°54′N, 66°35′W, 265 m, 4 specimens; 41°30′N, 69°00′W, 146 m, till, 1 specimen; 42°14′N, 69°57′W, 102 m, 1 specimen; 42°26′N, 66°28′W, 265 m, gravel, 8 specimens.

GENERAL CHARACTERISTICS.–The 9-28 mm high scapus is provided with white tubercles arranged in longitudinally oriented rows. The

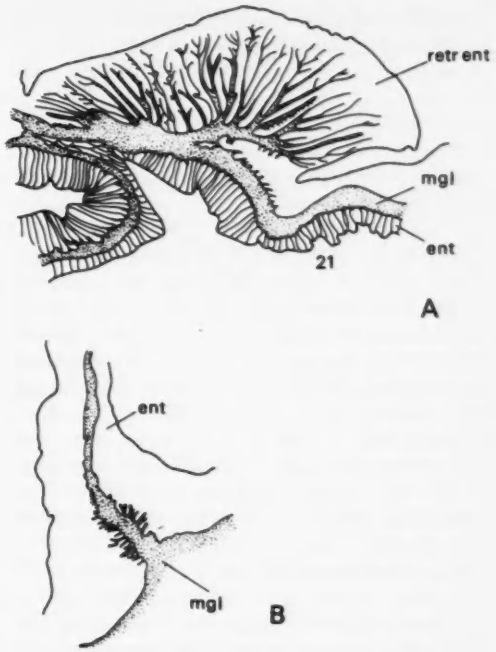


FIGURE 7.–*Sagartiogeton verrilli*. A. Section of the retractor of a perfect mesentery with adjacent parts of the actinopharynx. B. Section of the peripheral part of a mesentery (from the distal part of the scapus). ent–entoderm, mgl–mesogloea, retr ent–entoderm of retractor muscle.

scapular ridges are white and are 12 in number. The scapus is covered by a thin, greyish-white to greyish-brown periderm and is equipped with shallow longitudinal as well as transverse furrows; on the edge of the scapulus only radiating furrows are seen. The diameter of the column is 12-33 mm (diameter of scapus: diameter of the pedal disc = ca. 3:4). The tentacles are conical, reddish brown, and in older specimens longitudinally furrowed. They are 96 in number. The mesenteries have a maximum of 48 pairs (6+6+12+24), 6 of which (including the 2 pairs of directives) are perfect and sterile. The anatomical characters agree with earlier descriptions (cf. Carlgren 1893, 1933; Verrill 1922).

NEMATOCYSTS.–*Scapus*: basitrichs 8 × 1.1 - 11 × 1.6, 21-24 × 3.3-3.8; spirocysts 17 × 3.8 - 25 × 4.4. *Tentacles*: basitrichs 17 × 2.2 - 34 × 3.8; spirocysts 23 × 3.3-4.4 - 44 (56) × 5.4-7.6. *Actinopharynx*: basitrichs 16 × 1.6 - 35 × 3.3-3.8; microbasic *p*-mastigophors 23-33 × 3.8. *Fila-*

ments: basitrichs 14 × 1.1 - 16.4 × 1.6, 28 × 3.3 - 31 × 3.8-4.4; microbasic *p*-mastigophors 21 × 3.3 - 23 × 3.8. *Acontia*: basitrichs 32-40 × 3.8-4.4 μm.

Hormathia nodosa (?) (Fabricius 1780)

OCCURRENCE.–41°34′N, 68°40′W, 128 m, sandy silt, 1 specimen.

GENERAL CHARACTERISTICS.–The column is divisible into scapus and scapulus, the former being provided with a thin periderm and rather large, acuminated tubercles spread over the surface. The color of the scapus is proximally dark greyish brown, distally brown. Bordering upon the scapulus there are 12 large marginal tubercles. The pedal disc is not excavated; there are traces of mussel shell. The tentacles lack bulbous swellings on the abaxial side. They are arranged in four cycles. The actinopharynx and the sphincter agree with those in *H. nodosa* (cf. Carlgren 1893). The number of mesenteries is 96 (6+6+12+24 pairs), the perfect ones being 24 pairs in the distal part of the column. Immediately above the margin of the actinopharynx there are 20 pairs of perfect mesenteries. Only the six pairs of protomesenteries are sterile. The morphology of the retractors, parietobasilar, and basilar muscles agrees with that in typical *H. nodosa*. The length of the preserved specimen is: scapus 16 mm and scapulus 7 mm. The size of the pedal disc is 36 × 49 mm. The sizes of the different nematocyst types differ only slightly from those described in *H. nodosa* (see above). The large number of perfect mesenteries is, however, remarkable.

In view of the many morphological similarities between this specimen and typical *H. nodosa*, I consider it as an aberrant specimen of this species.

Actinauge verrilli McMurrich 1893

OCCURRENCE.–42°11′N, 65°56′W, 229 m, gravel, 1 specimen; 42°20′N, 67°28′W, 289 m, sandy gravel, 1 specimen; 42°50′N, 69°00′W, 187 m, sand-silt-clay, 1 specimen.

GENERAL CHARACTERISTICS.–The morphology of these specimens agrees with earlier descriptions of the species (cf. McMurrich 1893; Carlgren 1933). The scapus is equipped with a greyish-brown or brown periderm; it has a reticular appearance, arising from transverse as well as longitudinal, rather low, furrows. Distally there are 12 coronary tubercles. The firm wall of the scapulus is often whitish and is provided with 24, white, scapular ridges, proximally fusing two by two into 12. The scapus is cylindrical or dome-shaped, with the length 29-30 mm. The diameter of the scapus is proximally 17-30 mm and distally 19-20 mm. The length of the scapulus is 14 mm. The pedal disc is strongly excavated, often embracing sand grains. The long and tapering tentacles are arranged in four to five cycles. The outer tentacles are basally provided with abaxial swellings, which give rise to distinct processes. There are four cycles of mesenteries. Six pairs (including the two directive pairs) are perfect and sterile.

NEMATOCYSTS.–*Scapus*: basitrichs 8 × 1.6 - 23 × 4.4. *Tentacles*: basitrichs 12 × 2.2 - 27 × 2.7-3.3, ca. 40 × 3.8 (rare); microbasic *p*-mastigophors 24.5 × 3.8-5.2 - 38 × 8.2; spirocysts 19 × 3.3 - 37 × 4.4-6; 46-56 × 5.5-7. *Actinopharnyx*: basitrichs 13 × 1.6 - 17 × 2.2, 28-50 × 3.3; microbasic *p*-mastigophors 22 × 3.8 - 29 × 4.4. *Filaments*: basitrichs 11 × 1.1 - 17 × 2.2; 28-30.5 × 3.3, microbasic *p*-mastigophors 19 × 3.8-4.9 - 35 × 4.4. *Acontia*: basitrichs (14 × 2.2 -) 26 × 3.3 - 36.5 × 3.8-4.4 μm.

Phelliactis americana n. sp.

HOLOTYPE.–Specimen collected by the vessel *Delaware* from the type-locality (station number 27) on 19 February 1963 with an otter trawl. Deposited in the U.S. National Museum, catalog number USNM 54323.

TYPE-LOCALITY.–42°48′N, 63°42′W, 366 m, temperature +1.7°C.

PARATYPE.–Specimen collected by the vessel *Albatross IV* from station number 73 (42°17′N, 65°55′W, 238 m, gravel) on 15 August 1968 with a 1-m Naturalist dredge. Deposited in Northeast Fisheries Center, Woods Hole.

DIAGNOSIS OF HOLOTYPE.–Column firm, divisible into scapus and scapulus; somewhat asymmetric. Scapus distally with 48 rows of large, sometimes acute, tubercles. Scapular ridges about 70. Sphincter mesogloeal, and alveolar, very strong. Tentacles about 190, conical, and longitudinally furrowed with basal, abaxial swellings. Mesenteries in five cycles, 12 pairs being perfect

and sterile. Retractors of diffuse, restricted type. Parietobasilar muscles weak. Cnidom: *scapus* basitrichs; *tentacles* basitrichs and spirocysts; *actinopharynx* basitrichs and microbasic *p*-mastigophors; *filaments* basitrichs and microbasic *p*-mastigophors; *acontia* basitrichs.

GENERAL CHARACTERISTICS.–The column is firm and divisible into scapus and scapulus. It has a somewhat asymmetric appearance, one half of the body being larger than the other. The scapus (18 mm long) is cylindrical in the contracted state and has a reticular appearance with low tubercles formed by longitudinally as well as transversely oriented, low furrows; distally the scapus is provided with 48 rows of larger, sometimes acute, tubercles. The color of the remaining traces of periderm is brownish. The proximal part of the body is pillarlike, with the diameter 30 mm. About 70 scapular ridges are continued in the basilar swellings of the outer tentacles. The sphincter is rather short, but very strong, especially orally; it is alveolar and vertically stratified (Figure 8B). The actinopharynx is equipped with 12 longitudinal folds on each side of the two symmetrically arranged siphonoglyphs. The tentacles number about 190; they are rather short, conical, and longitudinally furrowed and are basally provided with abaxial swellings. The mesenteries are arranged in five cycles (6+6+12+25+50 pairs), 12 pairs (including the 2 pairs of directive mesenteries) being perfect and sterile. The retractors are of diffuse type, rather strong, and with their, in some perfect mesenteries, rather restricted pennons near to the actinopharyngeal wall (Figure 8C, D). The parietobasilar muscles are weak. The column, being somewhat wider distally than proximally, lacks cinclides. The whitish acontia are numerous and often very long. The mesogloeal layer is very thick in the whole column as well as in the mesenteries.

In the *paratype* the distal part of the column is in some parts severely damaged; the oral part is also introverted, giving rise to an oral slit, 58 mm long. The length of the scapus in this specimen is 40-30 mm; it is provided with low tubercles spread out over the column; distally there are 24 tubercles bordering the scapular ridges. The tentacles are arranged in four cycles (there are about 70 in the outer cycle) and are provided with abaxial swellings (Figure 8A). The mesenteries are hexamerously arranged in five cycles (the last cycle is, however, not complete in this specimen); proximally there are 75 pairs in total. The number of perfect and sterile mesenteries was impossible to determine in the paratype, but there are probably less than 12 pairs (probably 8). The wide and peripherally almost membraneous pedal disc is, to a small extent, excavated; its diameter measures 90 mm.

NEMATOCYSTS.–*Scapus*: basitrichs ca. 14 × 1.6-2.2, 24.5-44 × 3.3; spirocysts (not found in the paratype) 27 × 4.4 - 60 × 5.5. *Tentacles*: basitrichs 17-21 × 2.2 (not common), 34-43 × 3.3-3.8; spirocysts 38 × 4.4-4.9 - 75 × 8.7. *Actinopharynx*: basitrichs 16 × 2.2 (rare), 37 × 3.3 - 42 × 3.8; microbasic *p*-mastigophors 30 × 4.4 - 39 × 4.9. *Filaments*: basitrichs 12 × 1.6 - 22 × 2.2, 33 × 2.7 - 48 × 3.3; microbasic *p*-mastigophors 28 × 4.4 - 34 × 4.9. *Acontia*: basitrichs 16 × 2.2 - 23 × 2.5, 32 × 3.3 - 52 × 3.8 μm.

There are some morphological similarities between the above described specimens and *Phelliactis hertwigii* Simon as well as *Ph. incerta* Carlgren. The retractors of the perfect mesenteries are, however, stronger in *Ph. americana*, and the number of perfect mesenteries is larger (in the holotype 12 pairs).

Amphianthus nitidus (Verrill 1899)

OCCURRENCE.–41°27′N, 66°06′W, 128 m, 1 specimen; 41°39′N, 65°50′W, 183 m, 6 specimens; 42°10′N, 65°29′W, 163 m, 1 specimen.

GENERAL CHARACTERISTICS.–The column is firm, in the contracted state semispherical, and 9-16 mm high. The color is greyish white with a blue luster. The scapus is, in one of the studied specimens, equipped with eight low, extended tubercles. The diameter of the pedal disc is 12-16 mm. There is a distinct limbus. The tentacles are hexamerously arranged in four to five cycles (6+6+12+24+ a seldom completed fifth cycle), rather short, conical, and sometimes provided with an apical pore. The inner tentacles are larger than the outer ones. There are four to five cycles (57 pairs at most) of hexamerously arranged mesenteries, eight to nine pairs of which (including the two directive pairs) are perfect. All the mesenteries, except those of the last cycle and at least one of the directive pairs, are fertile. The number of mesenteries is larger proximally than distally. The acontia are numerous and yellow. The distally very strong, mesogloeal sphincter, the actinopharynx,

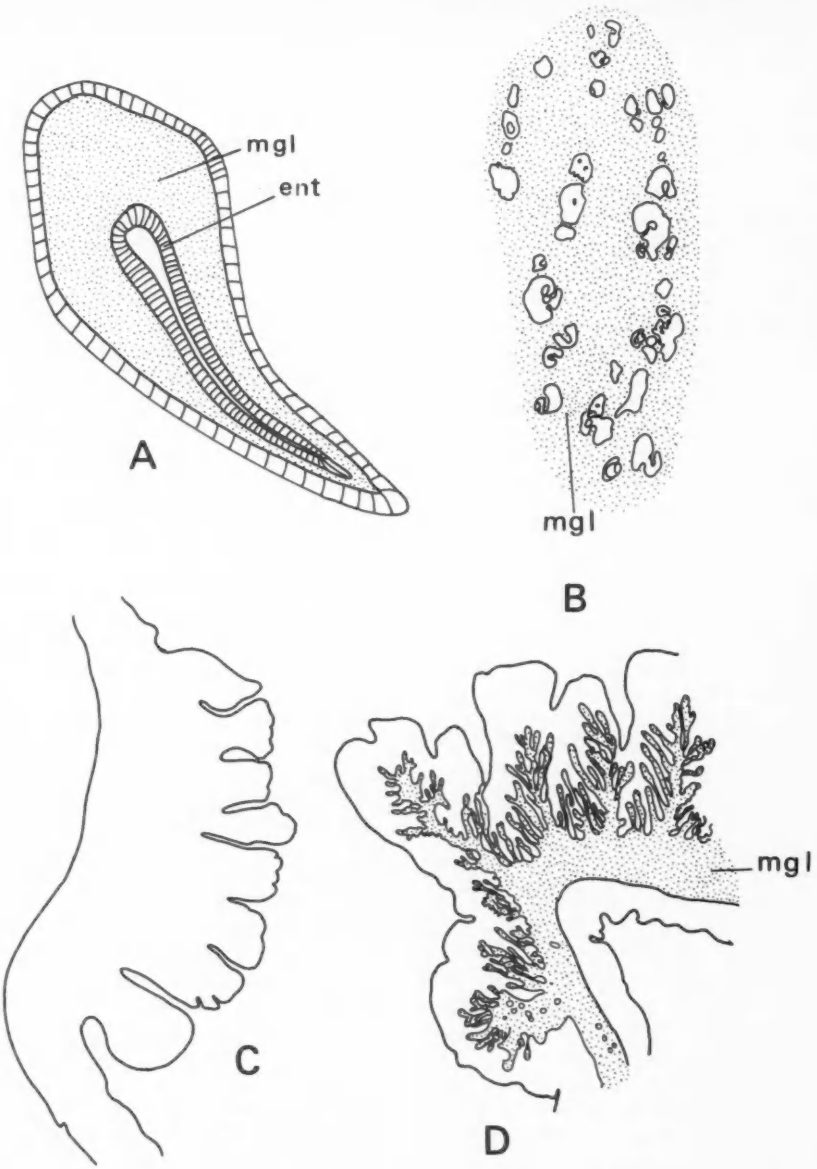


FIGURE 8.—*Phelliactis americana*. n. sp. A. Section through the basal part of a tentacle. B. Section through a part of the sphincter, showing the alveolar arrangement of the muscle fibrils (the fibrils are omitted in the figure). C. Section through a retractor from the third cycle of mesenteries. D. Cross section of a part of a retractor of one of the directive mesenteries. ent—entoderm, mgl—mesogloea.

and musculature of the specimens agree with earlier descriptions (cf. Carlgren 1934).

NEMATOCYSTS.–*Column*: basitrichs 8 × 1.6 - 12.5 × 2.7, 29-35 × 2.7; microbasic *p*-mastigophors 17 × 4.9 - 27 × 6; spirocysts 29 × 3.3 - 61 × 6. *Tentacles*: basitrichs 18.5 × 3.8 - 30 × 6; microbasic *p*(?)-mastigophors 18.5 × 4.4 - 29 × 4.4-5.5; spirocysts 19 × 3.3 - 47 × 7.6. *Actinopharynx*: basitrichs 24-25 × 3.3; microbasic *p*-mastigophors 23 × 4.4 - 26 × 5.5 (axial filament = about half the length of the capsule); ca. 27 × 4.9 (axial filament almost as long as the capsule). *Filaments*: basitrichs ca. 9 × 2.2; microbasic *p*-mastigophors 22 × 4.4 - 28 × 4.9. *Acontia*: basitrichs ca. 14 × 2.2; 42 × 6 - 57 × 6.5 μm.

Stephanauge nexilis **(Verrill 1883)**

OCCURRENCE.–41°54′N, 65°44′W, 366 m, 2 specimens; on the denuded axis of an octocoral.

GENERAL CHARACTERISTICS.–The yellowish, firm column is strongly elongated in the sagittal plane. The dimensions of the scapus is proximally 22 × 4 mm, the height of the column being 7 mm. In one of the specimens, the scapus is provided with 26 low, circularly arranged tubercles bordering 28 vague, radiating scapular ridges. The mesenterial insertions into the body wall are distinct. The number of the yellow, short, basally wide tentacles is not greater than that of the mesenteries (72 and 78). The sphincter is alveolar and strong, slowly diminishing in thickness towards the proximal part of the scapus. The wide actinopharynx is brownish yellow. It is equipped with two siphonoglyphs. The mesenteries are hexamerously arranged, more than six pairs (including the two pairs of directives) being perfect. At least some of the perfect mesenteries are equipped with genital organs. The retractors are diffuse and rather weak. The strong parietobasilar muscles produce distinct muscular lobes high up in the scapus, approximately at the middle of the mesenteries. The number of mesenteries is not greater proximally than distally. No acontia were found in these specimens (they might have been few and hidden by the strongly developed filaments), but basitrichs of probably acontian origin were measured in one of the specimens. No cinclides could be found.

NEMATOCYSTS.–*Scapus*: basitrichs (rare) ca. 12 × 2.2; microbasic *p*-mastigophors 12 × 4.4-5.5 - 19 × 5.5. *Tentacles*: basitrichs 9 × 1.7 - 20 × 2.7; microbasic *p*-mastigophors (axial filament almost as long as the capsule; diameter = 1.5 μm) 21 × 5.5 - 23 × 7.1; spirocysts 25 × 3.8 - 49 × 4.4. *Actinopharynx*: basitrichs 15-18 × 3.3; microbasic *p*-mastigophors 17 × 4.4 - 22 × 5.4-6. *Filaments*: basitrichs 14-16 × 2.7-3.3 (-28 × 2.7); microbasic *p*-mastigophors 16 × 3.8 (-6) - 27 × 5.5. *Acontia*(?): basitrichs 30.5-36.5 × 3.8 μm.

Hormathiidae (?)

Stephanauge (?) spongicola **(Verrill 1883)**

OCCURRENCE.–39°56′N, 69°45′W, 201 m, 3 specimens; 40°00′N, 69°30′W, 128 m, 3 specimens; 40°02′N, 70°47′W, 161 m, 6 specimens; 40°03′N, 71°16′W, 183 m, 16 specimens. At all the localities the specimens were found on the outside of the parchmentlike tubes of onuphid polychaetes.

GENERAL CHARACTERISTICS.–The column is often smooth but sometimes provided with a few adhesive warts; it is divisible into scapus and scapulus. The scapus was reddish brown to greyish brown in the preserved material, its length being 4-12 mm. The largest diameter is 10-11 mm. The scapulus is whitish to pale red. The periderm of the scapus is thin and easily falls off. The tentacles are conical, acute, and yellowish. They are hexamerously arranged in four to six cycles, those of the inner cycles being distinctly longer than the outer ones. The sphincter is short, mesogloeal, and agrees in its structure with that described by Carlgren (1950). It is not capable of covering all the tentacles. The actinopharynx is about three-quarters the length of the column, wide, and equipped with 18-20 deep, closely lying longitudinal folds (Figure 9A); it is yellowish in color. One (?) to four siphonoglyphs are present. In a specimen with two siphonoglyphs there was an eccentric position for them. There are (5-) 8-12 pairs of perfect mesenteries, the imperfect ones being 8-16 (-22) pairs. The structure of the retractors of the perfect mesenteries was in agreement with that described by Carlgren (1950) and in many ways reminiscent of those in *Phellia gausapata*. The number of directive pairs varies, being two, three, or four. The retractors of the perfect

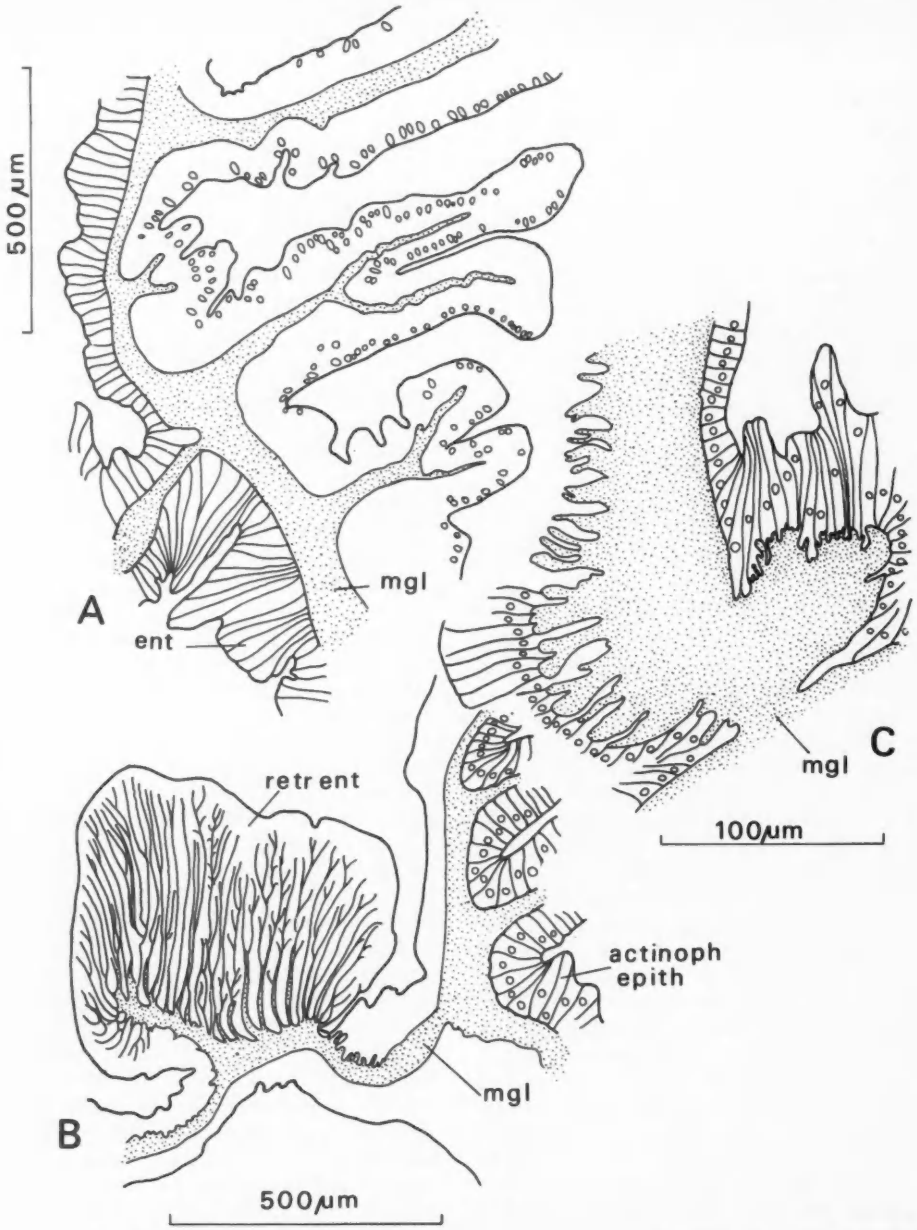
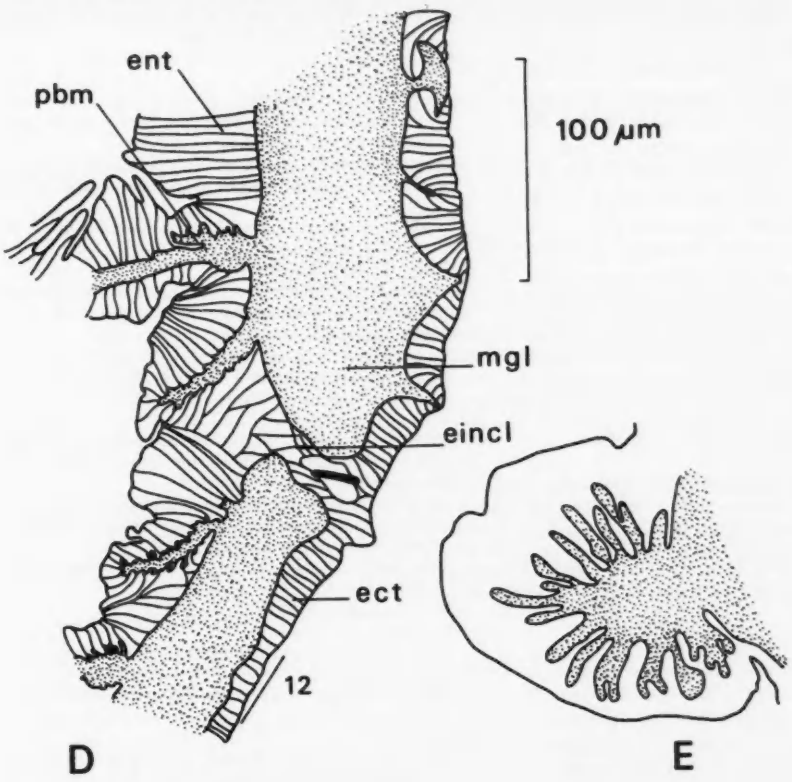


FIGURE 9.—*Stephanauge(?) spongicola*. A. Section through part of the actinopharynx. B. Cross section of a retractor of one of the protomesenteries. C. Cross section of the peripheral part of a perfect mesentery (the section is from the distal part of the column). D. Section through a part of the body wall. E. Section through a mesentery of the last cycle. actinoph epith—epithelium of actinopharynx, ect—ectoderm, eincl—ectodermal invagination forming an imperforate cinclis, ent—entoderm, mgl—mesogloea, pbm—parietobasilar muscle, retr ent—entoderm of retractor muscle.



mesenteries are strong, five to eight pairs being circumscribed, and sometimes reniform (Figure 9B), those of the other perfect mesenteries being diffuse but with a tendency to become restricted. The parietobasilar muscles are rather strong, forming distinct lamellae on the peripheral parts of the mesenteries (Figure 9C). The imperfect mesenteries lack retractors as well as filaments (always ?) (Figure 9E). In those specimens where genital organs were found, these were always developed in perfect mesenteries. The acontia are numerous and provided with basitrichs. Only one imperforate cinclis (Figure 9D) was found in the sections of the species. Probably the species reproduces asexually by laceration. The proximal part of the column and the often wide pedal disc are often asymmetrical.

NEMATOCYSTS.–*Column*: basitrichs (21 × 2.7 -) 23-27 × 3.3-3.8, 31-39 × 4.4; atrichs 19-20 × 4.4-4.9, 39-45 × 12.5-14.7. *Tentacles*: basitrichs 11 × 1.6-2.2 - 33 × 3.3-3.8; atrichs (not common; in many tentacles completely missing) 39 × 13.1 - 49 × 5.5, spirocysts (very numerous, and in some of the studied specimens with a very small variation in size) 17 × 2.2 - 34 × 3.8-4.9. *Actinopharynx*: basitrichs 14 × 2.2 - 32 × 3.8; microbasic *p*-mastigophors 17-26 × 3.8-4.4. *Filaments*: basitrichs 12-15 × 2.2; microbasic *p*-mastigophors 13 × 3.3 - 26 × 4.3-5.5. *Acontia*: basitrichs 13-16 × 2.2-2.7, 33 × 3.3 - 45 × 3.8 µm.

In specimens from 40°03'N, there were also found atrichs in the filaments (12 × 6, 18 × 4.9 - 24 × 5 µm) as well as holotrichs (22 × 4.9 - 24 × 5 µm). Both these nematocyst types are probably residues of intaken food–the specimens in question were found together with some individuals of *Epizoanthus incrustatus*.

This species, first described by Verrill (1883) as *Sagartia spongicola*, has been the object of later investigations by, e.g., McMurrich (1898) and Carlgren (1950). Carlgren (1950) (on the basis of acontian armament with basitrichs ?) described the species as a hormathiid and a member of the

genus *Stephanauge*, being aware of the existing anatomical differences in the development of the sphincter, the retractors, and the number of perfect mesenteries, siphonoglyphs, and directive mesenteries. To these differences should be added the occurrence of atrichous haplonemes, not only in the column ectoderm, but also in, at least, some of the inner tentacles. The arrangement of the mesenteries into filament-equipped perfect and into imperfect ones devoid of filaments as well as retractors should also be taken into consideration.

The morphology of this species shows so many differences from other species of the genus *Stephanauge* that I consider it very doubtful to place the species in this genus, or, taking into consideration the occurrence of atrichs in the studied specimens, in any other hormathiid genus.

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LITERATURE CITED

CARLGREN, O.
1891. Beiträge zur Kenntnis der Actinien-Gattung *Bolocera* Gosse. Öfvers. K. Vetenskaspakad. Förh. 48:241-250.
1893. Studien über Nordische Aktinien I. K. Sven. Vetenskaspakad. Handl. 25:1-148.
1931. Zur Kenntnis der Actiniaria Abasilaria. Ark. Zool. 23A(3), 48 p.
1933. The Godthaab Ezpedition 1928. Zoantharia and Actiniaria. Medd. Grønland 79(8), 55 p.
1934. Zur Revision der Actiniarien. Ark. Zool. 26A(18), 36 p.
1940a. A contribution to the knowledge of the structure and distribution of the cnidom in the Anthozoa. K. Fysiogr. Sällsk. Handl. Lund, N.F. 51:1-62.
1940b. Actiniaria from Alaska and Arctic waters. J. Wash. Acad. Sci. 30:21-27.
1945. Further contributions to the knowledge of the cnidom in the Anthozoa, especially in the Actiniaria. Lunds Univ. Arsskr., Ny Fobijl 41(9):1-24.
1949. A survey of the Ptychodactiaria, Corallimorpharia, and Actiniaria. K. Sven. Vetenskapsakad. Handl. 4(1): 1-121.
1950. A revision of some Actiniaria described by A. E. Verrill. J. Wash. Acad. Sci. 40:22-28.

CARLGREN, O., AND J. W. HEDGPETH.
1952. Actiniaria, Zoantharia and Ceriantharia from shallow water in the northwestern Gulf of Mexico. Publ. Inst. Mar. Sci. 2(2):141-172.

FIELD, L. R.
1949. Sea anemones and corals of Beaufort, North Carolina. Duke Univ. Mar. Stn. Bull. 5:1-39.

HAND, C.
1955. The sea anemones of central California. Part III. The Acontiarian anemones. Wasmann J. Biol. 13:189-251.

MCMURRICH, J. P.
1893. Report on the Actiniae collected by the United States Fish Commission steamer Albatross during the winter of 1887-1888. Proc. U.S. Natl. Mus. 16:119-216.
1898. Report on the Actiniaria collected by the Bahama Expedition of the State University of Iowa, 1893. Bull. Lab. Nat. Hist., State Univ. Iowa 4:225-249.

STEPHENSON, T. A.
1925. On a new British sea anemone. J. Mar. Biol. Assoc. U.K. 13:880-890.
1935. The British sea anemones. Vol. II. Ray Soc. (Lond.), Publ. 121, 426 p.

VERRILL, A. E.
1864. Revision of the *Polypi* of the eastern coast of the United States. Mem. Boston Soc. Nat. Hist. 1:1-45.
1867. Notes on the Radiata in the Museum of Yale College, with descriptions of new genera and species. Trans. Conn. Acad. Arts Sci. 1:247-596.
1883. Report on the results of dredging, under the supervision of *Alexander Agassiz*, on the east coast of the United States, during the summer of *1880*, by the U.S. Coast Survey steamer "*Blake*," *Commander J. R. Bartlett, U.S.N., commanding. XXI.* Report on the Anthozoa, and on some additional species dredged by the "Blake" in *1877-79*, and by the U.S. Fish Commission Steamer "Fish Hawk" in *1880-82*. Bull. Mus. Comp. Zool. 11(1):1-72.
1922. The Actiniaria of the Canadian Arctic Expeditions, with notes on interesting species from Hudson Bay and other Canadian localities. *In* A. E. Verrill (editor), Alcyonaria and Actinaria, p. 89-164. Rep. Can. Arctic Exped. 1913-18 8(G).

WEILL, R.
1934. Contribution à l'étude des cnidaires et de leurs nématocystes I-II. Trav. Stn. Zool. Wimereux 10-11:1-701.

DUAL STRUCTURAL EQUILIBRIUM IN THE FLORIDA SHRIMP PROCESSING INDUSTRY

JOSE ALVAREZ, CHRIS O. ANDREW, AND FRED J. PROCHASKA[1]

ABSTRACT

Stability, entry, exit, and mobility patterns for six size categories of firms in Florida shrimp processing industry for the 1959-71 period were studied by utilizing Markov Chain analysis. Forecasts over time predict that a structural equilibrium in the industry will be achieved by 1985. The forecasted changes in firm distribution suggest that Florida shrimp industry sales will become increasingly concentrated due to expansion in number of both small and large firms. A dual equilibrium, resulting in fewer medium-sized firms and more small- and large-sized firms, can be explained by the tendency for small firms to develop a specialty product and/or services in order to differentiate their markets from those of the very large firms. Medium-sized firms, then, tend to expand in size, or decline and either move to specialty products and services or exit from the industry.

Structural characteristics and patterns of Florida shrimp processing firms over the 1959-71 period, and the forecasts reveal several important structural characteristics of the industry. Entry into the Florida shrimp processing industry is relatively easy for small firms and more difficult for large firms. All firms are likely to move up in size by one only step or size category per time period. Exit from the industry in one time period is less probable for small and large firms than for medium-sized firms. Large firms are most likely to maintain their size between any two time periods and also experience less probability of declining in size than do medium- and small-sized firms.

Shrimp are the most important seafood processed in Florida. Total value of the shrimp processed in Florida in 1972 was slightly over $88 million. Processed shrimp products account for approximately 69% of Florida's total volume of nonindustrial seafood products and 70% of the value of seafood processed. In 1972, Florida's share of processed shrimp production in the southeast region was 28% (the southeast region representing about 75% of U.S. production). The growth of this industry was substantial during the last decade; both Florida's production and share of the U.S. market increased (Alvarez 1974).

Despite the growth in processing experienced by this industry, shrimp landings in the State declined significantly during the 1960-73 period. In 1960, 51 million pounds (23 million kg) of shrimp were landed; however, by 1973, landings declined to only 20 million pounds (13 million kg). Currently, the volume of shrimp processed in the State is three times as large as the volume of landings in the State, with the deficit being met by imports and non-Florida U.S. landings (Alvarez 1974). These comparisons indicate the basis of concern for the growth potential and nature of competition within the Florida shrimp processing industry. In a recent study addressing this concern (Alvarez 1974), emphasis was placed on processor sales concentration since there was evidence of "market power" in raw product purchases. The present study corroborates the findings of that study and further explains the results.

Predictions regarding future economic relationships are important to this industry for current managerial and investment decisions by firms and for long-run planning in optimizing firm size, scale economies, and product lines. Knowledge of the estimated number and size distribution of firms in the future will also help predict the character and intensity of competition within the market. Markov Chain analysis, employed in this study, is a useful tool for making such predictions. The analysis is a discrete-time stochastic process for which the state of the process at any time k depends only on the state of the processor at the immediately previous time $k - 1$. A Markov Chain is described by listing the states of the chain, the initial probabilities of being in various states, and the probabilities of transition from one state to another (Bishir and Drewes 1970).

The purpose of this paper is to analyze by size category the entry and exit patterns of firms in the Florida shrimp processing industry during the

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1959-71 period. The prevailing entry and exit patterns during the 1959-71 period are then used to forecast firm distribution over time and predict the equilibrium state of firms within the market. Results from a 1973 survey (Alvarez 1974) of the Florida shrimp processing industry are utilized in discussing the economic and managerial implications of entry and exit patterns identified in this analysis.

This study only considers shrimp processing firms and not handlers who deal exclusively with raw headless shrimp. Shrimp processors cook, peel and devein, and bread or prepare specialty shrimp products.

THEORETICAL CONSIDERATIONS

That market structure of an industry, according to Bain (1968), embodies the framework or conditioning environment within which specific enterprise behavioral characteristics evolve. This behavior encompasses both the market conduct and the market performance of firms. These conditions in turn influence the type of structural equilibrium achieved within an industry. The following brief paragraph discusses the market structure theory relevant to this paper.

Market structure is defined as "... those characteristics of the organization of a market which seem to influence strategically the nature of competition and pricing within the market" (Bain 1968). The number and size distribution of sellers, the conditions of entry, exit, and mobility within the industry are important aspects of market structure to be considered. The number of sellers specifies how many firms are competing for the buyer's dollar. Generally, an increase in the number of competing firms is indicative of a movement toward freer competition (Ward and Smoleny 1973). The size distribution of firms is generally measured by volume of sales or by the proportion of total output of the industry supplied by a firm or a group of firms. Conditions of entry are defined as the relative easy or difficulty with which new firms may enter the market, determined generally by the advantage or control which established firms exercise over potential entrants (Bain 1968). Mobility gives an indication of the ability for firms within an industry to make adjustments in their size and, therefore, is an indicator of the degree of structural rigidity within an industry (Ward and Smoleny 1973). Structural equilibrium is that point where net changes are no longer shown in the market structure. The number and distribution of firms remain fixed. Firm entry and exit occur at offsetting rates (Ward and Smoleny 1973).

ENTRY AND EXIT PATTERNS DURING THE 1959-71 PERIOD

Lack of time series data for total sales by individual firms necessitated use of employment data during the 1959-71 period as a measure of firm size (Florida State Chamber of Commerce 1959-71). A comprehensive research project based on a 1973 survey conducted by the authors showed that firm size measured by employment compared favorably with sales or volume as a measure of firm size (Alvarez 1974). Productivity per worker for firms with similar product lines (95% of industry sales) is quite similar to further corroborate this conclusion. Thus, employment is a good proxy for firm size in the shrimp industry.

The Florida shrimp processing industry is composed of several firms, each of a given size. The measurement of size as well as size categories (states of nature) are defined in this study as follows:

State	*Size of firm (employees)*	*Sales classification, 1972*	
1	0	–	–
2	1- 10	small	<$2 million
3	11- 30	small	<$2 million
4	31-100	medium	$2-12 million
5	101-300	medium	$2-12 million
6	>300	large	>$20 million

Thirty-one firms processed shrimp in Florida during the 1959-71 period. These firms and their respective states of nature throughout the entire period are presented in matrix form (Table 1) in 2-yr intervals because the data are only reported biannually. Rows in the matrix specify the different states of nature for each firm during the period under consideration. Firm number 2, e.g., with state 1 in 1959 and 1961 was not in business, then in 1963 entered the industry in state 6 (firm size of over 300 employees), maintained that size in 1965 and 1967, and exited from the industry in 1969. From the data contained in the matrix of Table 1, the transition matrix presented in Table 2 was calculated.

The probabilities on the transition matrix illustrate the stability (diagonal), entry (row one), exit (column one), and mobility (off diagonal) patterns

TABLE 1.–Total number of Florida shrimp processing firms and their respective states of nature[1] during the 1959-71 period.

Firm no.	1959	1961	1963	1965	1967	1969	1971
1	4	4	4	2	2	3	3
2	1	1	6	6	6	1	1
3	4	4	4	5	5	5	5
4	4	1	1	1	1	1	1
5	1	1	1	4	1	1	1
6	1	1	1	1	1	3	1
7	1	1	1	1	1	2	1
8	3	3	3	3	3	1	1
9	1	1	3	3	3	1	1
10	1	1	1	2	2	2	2
11	1	1	1	1	2	2	2
12	1	2	2	2	2	2	2
13	5	5	1	1	1	1	1
14	4	3	3	3	3	4	4
15	1	1	1	3	3	3	3
16	5	5	5	6	6	6	6
17	5	5	5	1	1	1	1
18	1	1	1	3	3	3	3
19	1	1	1	2	1	1	1
20	3	3	1	1	1	1	1
21	4	4	4	1	1	1	1
22	3	3	3	4	3	3	3
23	6	6	6	5	5	6	6
24	5	5	1	1	1	1	1
25	1	1	1	5	5	5	5
26	1	1	1	6	6	6	6
27	1	1	3	3	3	1	1
28	1	1	1	1	4	3	3
29	1	1	1	1	4	4	4
30	2	2	2	2	2	3	3
31	3	3	3	3	3	4	3

[1]For a definition of state of nature utilized in this study see text.

TABLE 2.–Transition matrix of the Florida shrimp processing industry.

Employees (number)		States of nature					
		1	2	3	4	5	6
0	1	0.8025	0.0617	0.0617	0.0370	0.0123	0.0247
1- 10	2	.1053	.7895	.1053	—	—	—
11- 30	3	.1351	—	.7838	.0811	—	—
31-100	4	.1667	.0556	.2222	.5000	.0556	—
101-300	5	.1667	—	—	—	.7222	.1111
>300	6	.0769	—	—	—	.0769	.8462

to delineate the structure of the Florida shrimp processing industry during the 1959-71 period. Each entry (P_{ij}) in Table 2 represents the probability of a firm moving from state i (row) to state j (column); e.g., P_{34} (0.0811) is the probability of a firm increasing in size from state 3 to state 4 in the next time period, and P_{42} (0.0556) is the probability of a firm decreasing in size from state 4 to state 2 in the following time period.

Industry stability, the probability of a firm maintaining the same size between any two successive time periods, is represented by numbers on the diagonal. The highest probabilities in the transition matrix are for shrimp processing firms to maintain the same size between any two time periods, suggesting that the industry is fairly stable. Firms of the largest size (state 6) are most likely to maintain their size. Medium-sized firms in state 4 are least stable, illustrated by an equal probability of remaining in the same size category or changing between any two periods.

Firm entry, specified in row one, is most probable for the smaller sizes (0.0167 for sizes 2 and 3) while the probabilities decrease for larger sizes.

Firm exit probabilities, shown in column one, are lowest for the largest and smallest firms.

Firm mobility, measured by increases or decreases in firm size, is shown by the off-diagonal numbers in the transition matrix. Shrimp processing firms of any size have at least some probability of moving one state upward at a time but almost zero probability of increasing in size by more than one state at a time. Moving downward in size scale is somewhat different. The largest firms (state 6) have a small probability of going from state 6 to 5, and zero of moving more than one state at a time. The second largest firms (state 5) have zero probability of moving down possibly because state 4 is not stable for various economic reasons. There are probabilities of declines by one or two states for firms of size 4 but a zero probability of decline from state 3 to state 2.

CHARACTERISTICS OF THE DUAL EQUILIBRIUM

Several important implications for the structure of the Florida shrimp processing industry can be drawn from the above description of the transition matrix, for the 1959-71 period. A dual equilibrium, created by instability of medium-sized firms and greater stability of small and large firms, is evident in the industry. Medium-sized firms are least stable as shown by the highest probabilities for either exiting from the industry or increasing or decreasing in size, and the highest probabilities for moving down more than two states in any time period. The dual equilibrium, with most stability for firms with less than 30 and for firms with 300 or more employees, is the result of a special characteristic of the Florida shrimp processing industry.

The largest firms may be able to exert some "market power" for a number of reasons. To be competitive, firms desiring to sell a general line of shrimp products must be sufficiently large to achieve the economies of scale in purchasing and processing presently experienced by large firms. Even though entry into the largest size is difficult, exit from that size in one time period is very unlikely. Size characteristics along with the high

probability of remaining in the largest state for a long period of time permit large firms to be more secure and ultimately more stable than small firms. Thus, large firms develop greater access to raw supply sources which are currently scarce, and greater knowledge of the national market accompanied by stability in supplying their customers.

Small firms, being able to enter with relative ease, find it very difficult to advance in size but remain in their state without too much difficulty. These firms are more likely to succeed if they produce specialty products, sell in isolated markets, or develop forward integration from shrimp fishing operations.

Firms of medium size, neither displaying the characteristics of large nor small firms, either exit from the industry or make adjustments in their size and/or product lines. Medium-sized firms tend to be unstable initially because they apparently are not organized to successfully enter shrimp specialty markets yet are too small to compete in the national major line shrimp markets.

FORECASTING FIRM DISTRIBUTION AND PREDICTING A STRUCTUAL EQUILIBRIUM

A forecast[2] for the 1961-71 period of the number of shrimp processing firms in each state of nature was conducted and compared with the actual number of firms appearing in the data during the same period (Table 3). The purpose of this procedure was to evaluate the appropriateness of the transition matrix for forecasting firm distribution within the industry.[3] When comparing actual firm numbers to predicted numbers in states 2 through 6 for 1961 through 1971, 17 of the 30 predictions were accurate and in state 4, which is least stable, 5 of the 6 predictions were accurate, giving confidence that the dual equilibrium structure remains intact with the predicted numbers.

[2]To forecast firm distribution in the Florida shrimp processing industry over time requires that the transition matrix be stationary; that is, the probabilities in the transition matrix do not change over time. Although, the chi-square "goodness-of-fit" test was conducted and the results show the transition matrix to be stationary, predictions should be considered tentative due to the small number of observations per cell caused by the low number of firms in the industry. Forecasted distribution, however, being very close to that found in the past, indicates that the transition matrix remains useful for prediction.

[3]Some of the differences may be due to the small number of observations or to rounding procedures.

Forecasting Firm Distribution Over Time

The biannual forecasted distribution of firm size for the Florida shrimp processing industry from 1973 to equilibrium appears in Table 3. Few changes in the number of firms in each state are observed. The smallest sizes (states 2 and 3) experienced an increase of one firm each while the remainder (states 4, 5, and 6) show no change. Thus, there is an increase of two in the total number of active firms. The number and size of firms in the industry will attain a structural equilibrium in a relatively short period of time.

Equilibrium State Within the Market

The equilibrium matrix for the Florida shrimp processing industry was calculated to show the final distribution of firms within the industry under the assumption of a stationary transition matrix (Derman et al. 1973). In equilibrium, firms may still enter and exit but neither the number of firms in each state of nature nor the total number of firms in the industry changes once the equilibrium is reached.

The distribution of firms in the equilibrium state compared with the distribution of firms

TABLE 3.–Actual number[1] of firms in each state of nature in the Florida shrimp processing industry, compared with the corresponding predicted numbers[2] using the transition matrix, 1959-71 and forecasting to 1985 and equilibrium.

Year		States of nature 1	2	3	4	5	6	Total no. active firms
1959		16	1	4	5	4	1	15
1961	a	16	2	5	3	4	1	15
	b	15	2	5	3	3	2	15
1963	a	16	2	6	3	2	2	15
	b	15	3	6	3	3	2	17
1965	a	11	5	7	2	3	3	20
	b	15	3	7	2	2	2	16
1967	a	10	5	8	2	3	3	21
	b	11	5	7	2	3	3	20
1969	a	12	4	7	3	2	3	19
	b	11	5	8	2	3	3	21
1971	a	14	3	7	2	2	3	17
	b	12	4	7	2	2	3	18
1973	b	13	3	7	2	2	3	17
1975	b	13	4	7	2	2	3	18
1977	b	13	4	7	2	2	3	18
1979	b	12	4	7	2	2	3	18
1981	b	12	4	7	2	2	3	18
1983	b	12	4	7	2	2	3	18
1985	b	12	4	8	2	2	3	19
Equilibrium[3]		12	4	8	2	2	3	19

[1]Data from source (Florida State Chamber of Commerce).
[2]Computed using the transition matrix.
[3]The equilibrium probabilities of transition in column order for the six states of nature were one (0.3881), two (0.1319), three (0.2454), four (0.0685), five (0.0603), and six (0.1058) for each of the six respective columns.

during the 1959-71 period (Table 3) shows that firms of the smaller sizes (states 2 and 3) increase in number as the industry reaches the structural equilibrium, while firms in states 4 and 5 decrease and firms in the largest size increase in number. This is a consequence of the industry dual equilibrium conditions of entry and exit identified in the 1959-71 period.

At the structural equilibrium, and in support of the dual equilibrium, the probabilities for firm entry are highest for firms with less than 30 employees and for those with more than 300 employees. Thus, the least amount of entry activity will occur within the medium-sized firms.

Mean Lifetime for Each Size Category

Mean lifetime values for each size category were calculated (Table 4) and further support the prevalence of a dual equilibrium in the Florida shrimp industry. Mean lifetime represents the number of years a firm tends to stay in a given state of nature. The largest firms tend to maintain their size for a greater number of years (13) than firms in any other size category. Firms of sizes 2 and 3 have mean lifetime values of 9 yr, while firms of size 4 and size 5 tend to remain for an average of 4 and 7 yr in their respective states. These findings are the result of the firms' probabilities of maintaining their size between any two time periods. Column 2 of Table 4 represents the number of years spent in each size for an equilibrium distribution (perfectly mobile industry); the values are very similar. The data in Column 3 indicate state rigidity where the smaller the ratio, the more rigid the state. State 6 is the most rigid state in the industry, followed by states 2, 3, 5, and 4, respectively.

TABLE 4.—Mean lifetime in years for each size category for the Florida shrimp processing industry[1]

States of nature[2]	Column 1 Average[3] (yr)	Column 2 Perfect[4] (yr)	Column 3 Ratio[5]
2	9.500	2.304	0.243
3	9.250	2.650	.286
4	4.000	2.418	.604
5	7.200	2.128	.296
6	13.000	2.236	.172

[1]Mean lifetime represents the number of years a firm tends to stay in a given size category. In this case, results were multiplied by 2 since each time period equals 2 (yr) in the data.

[2]State 1 is not included because it is an absorbing state.

[3]Calculated from the transition matrix with the formula $(1/1 - P_{ii})$.

[4]Time spent in each state for a perfectly mobile industry as calculated from the equilibrium size distribution.

[5]Column 2 ÷ Column 1.

LITERATURE CITED

ALVAREZ, J.
1974. The Florida shrimp processing industry: Economic structure and marketing channels. M.S. Thesis, Univ. Florida, Gainesville, 168 p.

BAIN, J. S.
1968. Industrial organization. John Wiley and Sons, Inc., N.Y., 678 p.

BISHIR, J. W., AND D. W. DREWES.
1970. Mathematics in the behavioral and social sciences. Harcourt, Brace & World, Inc., N.Y., 714 p.

DERMAN, C., J. G. LEON, AND O. INGRAM.
1973. A guide to probability and application. Holt, Rinehart, and Winston, Inc., N.Y., 750 p.

FLORIDA STATE CHAMBER OF COMMERCE.
1959-71. Directory of Florida industries. Florida State Chamber of Commerce, Jacksonville, Biannual Issues.

WARD, R. W., AND C. SMOLENY.
1973. The market structure of Florida fresh grapefruit packers: An application of Markov Chain analyses. Econ. Res. Dep. 73-1, Fla. Dep. Citrus and Univ. Fla, Gainesville, 91 p.

DISTRIBUTION AND ECOLOGY OF PELAGIC FISHES STUDIED FROM EGGS AND LARVAE IN AN UPWELLING AREA OFF SPANISH SAHARA

MAURICE BLACKBURN[1] AND WALTER NELLEN[2]

ABSTRACT

Fish eggs and larvae were taken in vertical zooplankton hauls in a small upwelling area off Spanish Sahara. Series of hauls were made repetitively from March to May 1974, sometimes with accompanying hydrocasts. About 58% of the eggs and 72% of the larvae belonged to the following pelagic species: *Sardina pilchardus*, *Engraulis encrasicholus*, *Trachurus* spp., and *Maurolicus* sp. It was estimated from contemporaneous current meter data and other information that the eggs of those species were spawned very close in time and space to where they were collected. Thus adult *Sardina* and *Engraulis* appeared to occur typically on the continental shelf, adult *Trachurus* at the edge of the shelf, and adult *Maurolicus* over the continental slope. These distributions were verified for *Sardina* and *Trachurus* from fishing results of Polish vessels. Acoustically detected concentrations of fish were identified by species according to those results.

The area of abundance of *Sardina* was characterized by maxima of phytoplankton and small zooplankton. Abundance of *Sardina* eggs changed with time, because of variations in the size of the adult population in the area (acoustically estimated) and in its production of eggs. The major change in population size coincided with a similar change in the amount of food, especially phytoplankton, available. Variations in egg production may have been associated with the mean temperature in the water column, since eggs were scarce when the mean was below 16.5°C even when adults were abundant.

A multidisciplinary group of U.S. scientists made an oceanographic study off Spanish Sahara from March through May 1974. The program is called Coastal Upwelling Ecosystems Analysis (CUEA) and is part of the International Decade of Ocean Exploration (IDOE). The operation off Spanish Sahara (Figure 1) was called JOINT-I. It made observations of many kinds over an upwelling area which was small enough to be studied synoptically in great detail repetitively under various conditions such as changes in the wind field. Most of the work was done from the coast to long. 18°00′W, between lat. 21°30′ and 21°50′N. The continental shelf in this area is bounded by the 100-m isobath, beyond which there is a steep slope (Figures 2-4).

Pelagic fish are a major component of the animal biomass in the area. They support large fisheries conducted by several nations. It was the task of a small group of CUEA investigators to estimate biomass of pelagic fishes by species and, if possible, by trophic levels during JOINT-I; to show the distributions of these biomasses in space and time;

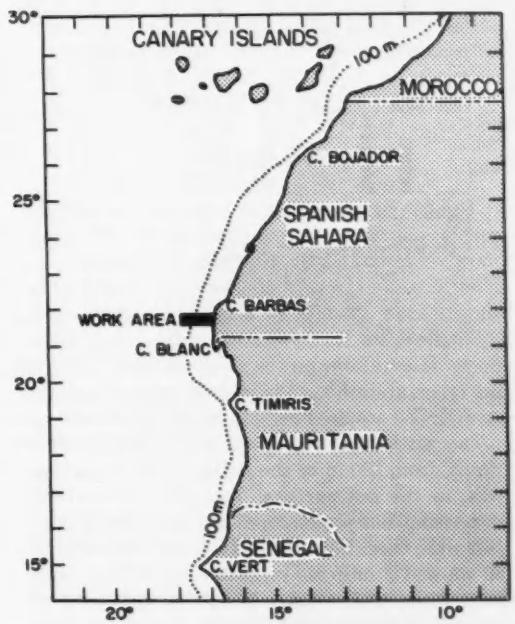

FIGURE 1.—Part of northwest Africa showing the principal area of JOINT-I work.

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and to explain the distributions in terms of environmental parameters. Biomass of total pelagic fish was estimated acoustically (Thorne et al. in press). Partitioning it by species was to be based on the following: contemporaneous catches by fishing or fishery research vessels, samples of fish taken by the CUEA ships, fish eggs and larvae from the zooplankton catches of the CUEA ships, and the literature. In the outcome, only the fish eggs and larvae (ichthyoplankton) were useful during the cruise. Good information on fish catches by other vessels was not received until many months later, sampling from the CUEA ships was unproductive for adults of epipelagic species, and the literature did not resolve all questions. The ichthyoplankton results and the fish catches agreed as to the principal species present in different parts of the area. Acoustically detected concentrations of fish (Thorne et al. in press) were identified accordingly.

This paper gives the principal results of work on the eggs and larvae. It then uses the egg distributions to estimate contemporaneous distributions of adults of some species and compares those with data from contemporaneous fish catches and the literature. Finally the paper attempts to explain the distributions of an abundant species, *Sardina pilchardus* (Walbaum), according to environmental data collected at the same time as the eggs.

MATERIAL AND METHODS

Zooplankton

The fish eggs and larvae were sorted from the zooplankton catches made during JOINT-I and partly identified by Blackburn. Most of the identifications were made later by Nellen. The zooplankton catches were made and processed, apart from the ichthyoplankton, by R. I. Clutter. Some observations on the zooplankton in general are relevant in this study. A more complete report on JOINT-I zooplankton will appear elsewhere.

The net hauls for zooplankton were made vertically from 200 m or the bottom, whichever was less, to the sea surface. Two cylindro-conical, nonclosing Bongo plankton nets mounted side by side were used. Each net had a mouth diameter of 60 cm and a uniform mesh size of 102 μm. Nets were lowered at 40 m/min and hauled up at 60 m/min. A calibrated digital flowmeter was mounted in the mouth of each net. Volume of water filtered by the two nets ranged from 12 to 158 m^3, depending mainly upon the haul length. Only one net was used in series 1 and 2 (Table 1).

Processing was as follows, with exceptions shown in footnotes to Table 1. The catches from the two nets were immediately combined and suspended in water. The suspension was shaken and four ¼-aliquots were decanted. Each of two aliquots was filtered through a series of sieves (mesh sizes 1,050, 505, 223, and 102 μm) until no more water dripped. This procedure yielded subsamples of zooplankton in four size ranges, approximately 100 to 200, 200 to 500, 500 to 1,000, and > 1,000 μm. The subsamples from one aliquot were scraped from the filters, blotted on paper towels until no more water appeared, and weighed. The subsamples from the other aliquot were washed off the filters and preserved in Formalin.[3] The fish eggs and larvae were sorted from the preserved 500- to 1,000- and >1,000-μm samples and combined. The four wet weights per haul were standardized in grams under 1 m^2 of sea surface. Allowance was made trigonometrically for effects

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

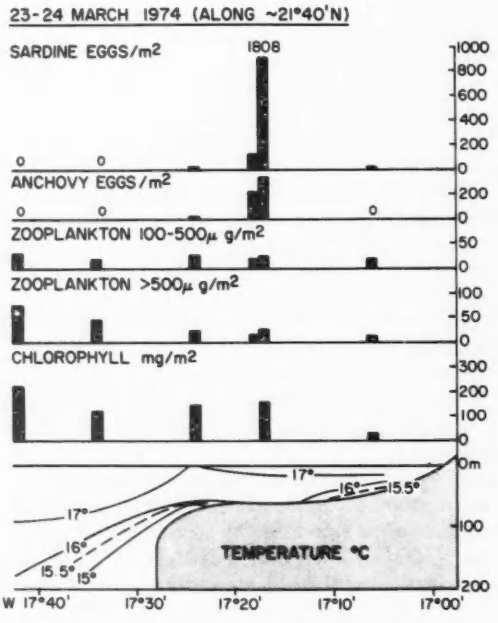

FIGURE 2.—Distribution of sardine eggs, anchovy eggs, and environmental parameters along lat. 21°40'N on 23-24 March 1974 (series 5 in Table 1).

TABLE 1.—Means of variables for the water column at stations from long. 17°08′ to 17°25′W, in series of stations along lat. 21°40′N together with indications of relative abundance of adult sardines explained in Discussion.

Series	Date 1974	No. of stations	Sardine eggs/m²	Anchovy eggs/m²	Temp. °C	Chlorophyll (mg/m²)	Small zooplankton (g/m²)	Abundance of adult sardines
1	8- 9 Mar.	[1]4	10	1	16.5	115	[2]85	Low
2	10-11 Mar.	[3]4	4	0	16.5	30	[2]90	Low
3	15-17 Mar.	[4]4	0	0	16.0	193	[5]78	([6])
4	18 Mar.	3	5	30	16.0	71	[5]27	([6])
5	23-24 Mar.	3	648	195	16.5	164	20	High
6	1- 2 Apr.	2	0	57	16.5	52	19	Low
7	5 Apr.	3	8	5	15.5	187	24	Medium
8	12-13 Apr.	[7]3	54	36	17.0	147	32	Medium
9	22-23 Apr.	3	7	19	16.0	192	28	Medium
10	9-10 May	4	431	2	16.5	323	53	High

[1]Three stations for eggs and zooplankton.
[2]Estimated from settled volumes at 1 ml = 0.8 g. Not corrected for phytoplankton contamination.
[3]One station for chlorophyll.
[4]Two stations for eggs and zooplankton.
[5]Estimated according to mean ratio of small to total zooplankton at same longitudes in other series, namely 67%. Not corrected for phytoplankton contamination.
[6]Unknown.
[7]Two stations for chlorophyll.

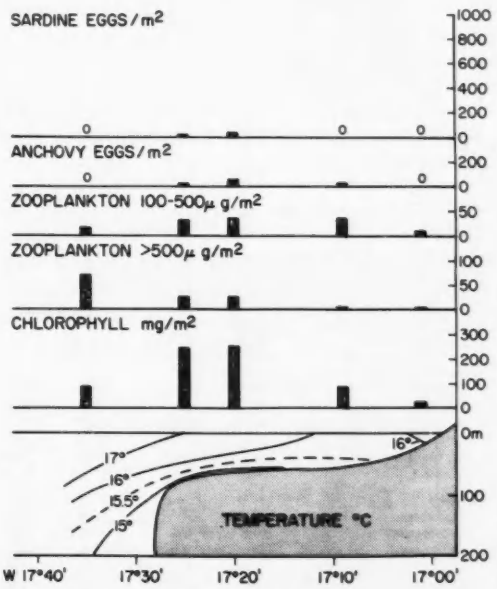

FIGURE 3.—Distribution of sardine eggs, anchovy eggs, and environmental parameters along lat. 21°40′N on 22-23 April 1974 (series 9 in Table 1).

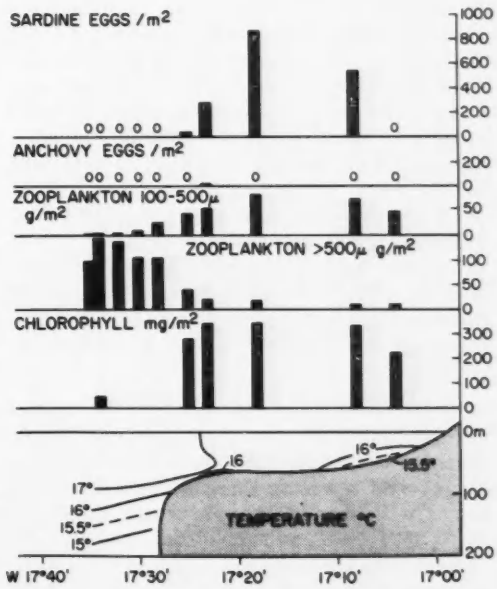

FIGURE 4.—Distribution of sardine eggs, anchovy eggs, and environmental parameters along lat. 21°40′N on 9-10 May 1974 (series 10 in Table 1).

of nonzero wire angles on distance covered by the net. To determine effects of clogging, the expected flow of water through the net was compared with that indicated by the flowmeter revolutions. Counts of various kinds of fish eggs and larvae from each haul were standardized in numbers under 1 m² of sea surface.

In general the spatial distribution of zooplankton biomass was similar for the 100- to 200- and 200- to 500-μm fractions. The two fractions of larger-sized plankton were also distributed similarly, but not like the smaller-sized fractions. Thus we distinguish only zooplankton at 100 to 500 μm and at >500 μm (Figures 2-4). Most of the

biomasses given here, but not all (see Table 1), have been corrected for contamination by phytoplankton. The correction was made as follows. The amount of chlorophyll *a* was determined in a ¼-aliquot by SCOR methods (UNESCO 1966) and partitioned among the four subsamples according to inspection of the preserved samples. The inspection indicated approximate relative amounts of phytoplankton in the samples. The chlorophyll weight for each subsample was converted to carbon following Lorenzen (1968) and then to wet weight according to Cushing et al. (1958). The correction generally reduced the original biomass by less than 10% but occasionally up to 30%. All biomasses shown in Figures 2 to 4 have been corrected.

The preserved samples of zooplankton <500 μm were not examined for ichthyoplankton, because few specimens (except some newly hatched larvae) were expected to pass through a 500-μm sieve. For eggs of Engraulidae, which are oval and measured from 500 to 580 μm (mean 570 μm) in transverse diameter in our material, our numbers per haul could have been slightly too low because of losses through the 500-μm sieve. It is unlikely that these losses were high. During a later cruise (AUFTRIEB 1975) in the same area, we counted engraulid eggs in the catches of two Bongo nets of uniform mesh sizes, 300 and 500 μm, but otherwise identical and hauled side by side in the same net assembly. Egg numbers were 122 and 145, so the 300-μm net retained no more than the 500-μm net.

Temperature and Chlorophyll *a*

These properties were measured from hydrographic casts which used plastic 5-liter Niskin bottles with reversing thermometers. Sampling depths in the upper 200 m were usually 0, 3, 10, 20, 30, 50, 75, 100, 150, and 200 m, depending on the bathymetry. Concentrations of chlorophyll *a* were determined by SCOR methods (UNESCO 1966) and integrated in milligrams per square meter. The integration program summed the area of each depth integral using the area formula of a trapezoid. Samples for chlorophyll *a* were generally not taken below 75 or 100 m, because results of other casts showed little chlorophyll below those depths.

Area and Periods of Study

Almost all the zooplankton hauls and hydrographic casts of JOINT-I were made in the area shown in Figures 1 and 5. They were generally made along an east-west line at about lat. 21°40′N, where series of hauls and casts (not always together) were frequently repeated. Figure 5A shows the positions of all zooplankton hauls made in the area. Nine other hauls were scattered in space and time in adjacent areas, and are not used in this paper. No distinction is made here between day and night hauls. Hauls on the shelf were made mostly by day and those on the slope mostly at night. Eggs are of more interest than larvae in this study as explained above and should have been equally available by day and night. Larvae might have avoided the nets more by day than by night.

The total period of JOINT-I in which zooplankton hauls were made was 8 March to 10 May 1974. It was divided by port calls into three parts, Legs 1, 2, and 3 (Table 2). The periods of these legs (first to last zooplankton haul) were 8 to 24 March, 1 to 14 April, and 22 April to 10 May.

Ten series of hauls were made together with hydrographic casts along lat. 21°40′N, each series occupying 1 to 3 days. Figures 2 to 4 show data for some of the series and Table 1 summarizes data for all of them.

TABLE 2.—Principal categories of fish eggs and larvae taken on JOINT-I in the area of Figure 5, showing numbers per square meter averaged for hauls on each leg of the cruise and summed for the cruise.

Category	Leg 1 (41 hauls)	Leg 2 (22 hauls)	Leg 3 (38 hauls)	Cruise total No.	Cruise total %
Eggs:					
Sardina	77.7	10.9	75.9	6,308	35.1
Engraulis	19.0	16.1	14.8	1,695	9.4
Maurolicus	6.2	29.3	15.4	1,487	8.3
Soleidae	9.9	15.0	8.8	1,071	6.0
Carangidae	4.8	0.7	18.1	897	5.0
Others	55.3	56.1	79.8	6,531	36.2
Larvae:					
Clupeoidei	60.5	82.9	84.7	7,522	69.7
Heterosomata	24.1	16.5	5.0	1,541	14.3
Sparidae	6.6	22.6	9.3	1,120	10.4
Maurolicus	1.2	1.3	2.8	185	1.7
Myctophidae	0.9	0.7	1.3	102	0.9
Carangidae	0.4	2.1	0.4	78	0.7
Others	3.5	2.3	1.5	251	2.3

IDENTIFICATION AND ENUMERATION OF EGGS AND LARVAE

The eggs and larvae from all stations in Figure 5A were identifiable in the categories shown in Table 2. Most of the identifications were made at the Institut für Meereskunde from the large collections, literature, and experience of northwest

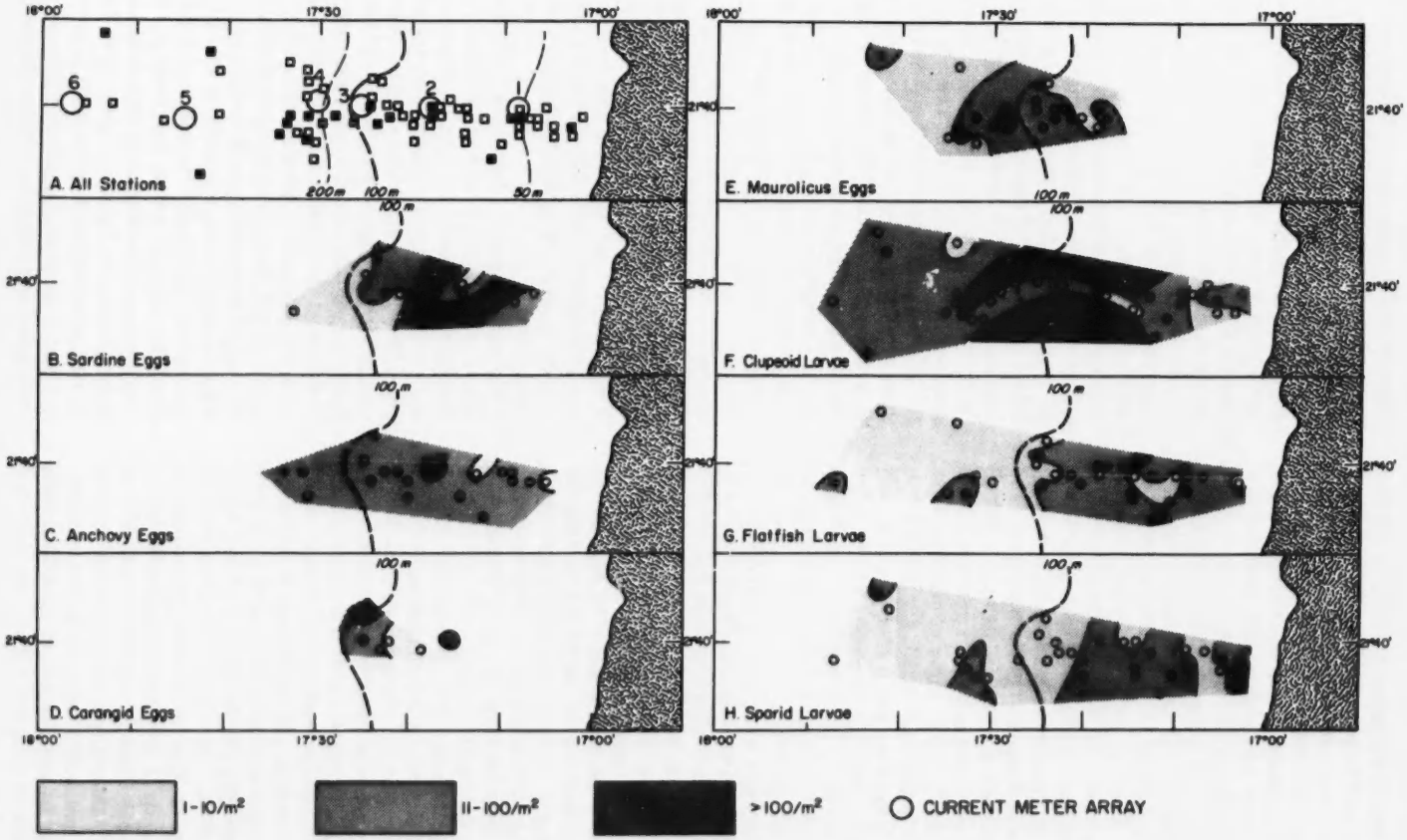

FIGURE 5.—Distributions of fish eggs and larvae from the zooplankton of JOINT-I, between lat. 21°30′ and 21°50′N. A. Positions of all zooplankton hauls. Solid squares show where hauls were repeated. Circles show current meter arrays. B to H. Positions of positive hauls for kinds of eggs and larvae stated, contoured in numbers per square meter.

African ichthyoplankton available there. Identifications of larvae were more complete than those of eggs, as is usual in work of this kind.

Among the eggs the following kinds, which are well known in literature because of conspicuous characters, were easily identified: *Sardina*, *Engraulis*, *Maurolicus*, and Soleidae.

The eggs of *Sardina* and *Sardinops* are alike but the only species of either genus recorded off northwest Africa is *Sardina pilchardus* (Walbaum). *Sardina pilchardus* occurs off southwestern Europe, in the Mediterranean, and on the coast of northwest Africa as far south as lat. 20°N (de Buen 1937; Larrañeta 1960; Maurin 1968; Furnestin and Furnestin 1970). We identify the eggs as that species, which we later call "sardine." Egg diameters in our material range from 1.33 to 1.50 mm (mean 1.46 mm), slightly lower than those of the same species in the Mediterranean (1.40 to 1.70 mm; Larrañeta 1960). However they are considerably larger than those of *Sardinella*, the other clupeid genus that might occur, whose eggs measure 1.1 to 1.3 mm off west Africa (Marchal 1967).

Engraulid eggs were easily recognizable by their oval shape. Two species of Engraulidae have been reported off southern Spanish Sahara, *Engraulis encrasicholus* (Linnaeus) and *Anchoa guineensis* (Rossignol and Blache) (Lozano Cabo 1970; Bravo de Laguna Cabrera and Santaella Alvarez 1973). No adults were obtained during JOINT-I, so identification has been made from the eggs. Eggs of *E. encrasicholus* range from 0.90 to 1.9 mm in length and 0.42 to 1.2 mm in maximum breadth (Demir 1963); corresponding ranges for *A. guineensis* are 1.05 to 1.23 and 0.54 to 0.58 mm, respectively (Marchal 1966), and for our material 1.33 to 1.50 and 0.50 to 0.58 mm, respectively. Our eggs could belong to either species as far as breadth is concerned, but only to *E. encrasicholus* on the basis of length. We refer to this species later as "anchovy." It occurs off western Europe and in the Mediterranean and Black seas, as well as off northwest Africa, where its southern limit is not exactly known (de Buen 1931 and references above).

The eggs of *Maurolicus* (family Gonostomatidae) are those of *M. muelleri* (Gmelin), which has been recorded off southern Morocco and northern Mauritania (Maurin et al. 1970). The eggs of Soleidae could belong to several species recorded off Spanish Sahara (Maurin et al. 1970; Lozano Cabo 1970).

The carangid eggs were identified with help from E. H. Ahlstrom, who noted that some of them resembled *Trachurus*. They measured about 0.9 to 1.0 mm, in the size range reported for *T. trachurus* (Linnaeus) off northwest Africa (Kiliachenkova 1970). Three other species of *Trachurus* have been recorded off northwest Africa, namely *T. picturatus* (Bowdich), *T. trecae* Cadenat, and *T. mediterraneus* Steindachner. *Trachurus picturatus* is not common and *T. mediterraneus* may be a subspecies of *T. trachurus* (Letaconnoux 1951; Maurin et al. 1970; Witzell 1973). The three most common carangids in the area of Figure 1 are *T. trachurus*, *T. trecae*, and *Caranx rhonchus* Geoffroy St. Hilaire. The first two spawn off Spanish Sahara from about November to April, and *C. rhonchus* from about May to August (Boely et al. 1973). Aboussouan (1967) and Conand and Franqueville (1973) described larvae of these species. The distinctions between larvae of *Trachurus* and *C. rhonchus* are slight and the larvae of the two *Trachurus* species cannot be distinguished. Most of our carangid eggs are probably *Trachurus* ("horse mackerel"), which was abundant along the coast of Spanish Sahara between March and June 1974. The most likely species is *T. trachurus*. All specimens of *Trachurus* taken in research trawling during JOINT-I were that species. We took 22 post-larval and juvenile *Trachurus* up to 6 cm long in various hauls of a micronekton net during JOINT-I. All specimens large enough to be identified were *T. trachurus*. We identified carangid eggs conservatively and so may have failed to count some.

The remaining eggs, 36% of the total, were of several kinds not readily identifiable by us. Probably few of them were eggs of pelagic species, except possibly some carangids as suggested above. They lacked segmented yolks and thus were probably not Isospondyli. *Scomber japonicus* Houttuyn is a pelagic species that spawns mostly from December to February in the vicinity of Cap Blanc (references in Blackburn 1975). If *Scomber* eggs occurred in our collections, they were probably not abundant. We found no *Scomber* larvae. Other abundant pelagic species of the JOINT-I area spawn principally in summer (Blackburn 1975). Thus unidentified eggs probably were mostly demersal species, as were 25% of larvae, i.e., Heterosomata and Sparidae, as shown in Table 2. Spatial distribution of unidentified eggs resembled that of the demersal larvae (Figure 5G, H).

All larvae were identified to some taxon. Closer

identifications could have been made in some cases but were not needed for this study. Clupeoids predominated. Many clupeoids were small (about 5 to 10 mm) and had lost part of the intestine, probably because of the repeated filtering of the zooplankton. Clupeidae and Engraulidae were not separately counted, but both families were well represented. Preanal myomeres were counted in randomly selected good clupeid specimens. These counts ranged from 41 to 43, which agree with *Sardina pilchardus* (Saville 1964). Comparable ranges in two other west African clupeids, *Sardinella aurita* Valenciennes and *Sardinella eba* (Valenciennes), are respectively 38 to 41 and 35 to 38 (Conand and Fagetti 1971). These species were looked for because Maigret (1972) found *Sardinella* larvae near the area of JOINT-I in May. Evidently they were absent or scarce in our material. They were absent or scarce in the 1974 fish catches reported to us. We conclude that our clupeoid larvae were *Sardina pilchardus* and *Engraulis encrasicholus*, like the clupeoid eggs. Carangid larvae were scarce. Larvae in the last line of Table 2 ("Others") were *Merluccius*, *Callionymus*, Paralepididae, and Anguilliformes (leptocephali).

Table 2 shows that *Sardina* dominated the egg samples. It shows also that abundance of *Sardina* eggs varied greatly during JOINT-I, which is discussed later.

SPATIAL DISTRIBUTION OF EGGS AND LARVAE

Figure 5B-H shows distribution and abundance of the principal kinds of eggs and larvae identified, during the whole period of cruise JOINT-I. All positive hauls for each kind were charted and the observed numbers per square meter were contoured without averaging. The purpose of Figure 5 is to show where maxima and minima occurred, although some of them were more prominent at those locations on some legs of the cruise than on others. For example the midshelf maximum of *Sardina* eggs was not prominent on Leg 2, when eggs were scarce everywhere (cf. Tables 1, 2). We were most interested in the pelagic species and especially in their eggs, whose distributions should be close to those of the adults. Furthermore, the methods employed were more suitable for eggs than larvae. Some larvae could have avoided the nets, especially in daytime.

Sardine and anchovy eggs were absent close inshore, most abundant on the continental shelf between the 50- and 100-m isobaths, and occasionally found just beyond the shelf edge (Figure 5B, C). These eggs occur most abundantly in the uppermost 25 m of the water column (Furnestin and Furnestin 1959; Larrañeta 1960; Demir 1963), where temperatures on JOINT-I were about 16° to 17°C (Figures 2-4). The eggs take about 3 days to hatch at such temperatures (Larrañeta 1960; Demir 1963), so their average age should be about 1.5 days.

Six vertical arrays of current meters were moored during JOINT-I (Figure 5A). No ichthyoplankton were collected near array number 6. The other arrays operated for periods of about 20 days (number 3) to 60 days (number 2). Means of the meridional and zonal components of water movement, v and u, are available for each current meter during the period of operation (Pillsbury et al. 1974). The top meter in each array was about 20 m below the surface. At this depth, mean v was about 20 cm/s on the continental shelf (arrays 1 and 2) and 10 cm/s on the edge and slope (arrays 3, 4, and 5), towards the south. Mean u was about 2 cm/s towards the west, except at array 3 where it had the same velocity towards the east. Thus, from where it was spawned by the parent, a sardine or anchovy egg of average age on the continental shelf could have drifted about 14 nautical miles to the south and 1.4 miles to the west. The movement to the west is negligible for our purpose. The coastline and isobaths run generally north and south along this section of the coast, as do isopleths of surface temperature and surface nitrate concentration (Voituriez et al. 1974; D. W. Stuart and J. J. Walsh, pers. commun.). Thus the parent fish probably occurred over the same bathymetry and under the same environmental conditions as the eggs did, but slightly farther north.

Carangid eggs (Figure 5D) were found on the outer half of the shelf, especially at the edge. Kiliachenkova (1970) found eggs of *Trachurus trachurus* distributed in exactly the same way in the same area in November, December, and May. The literature does not clearly show the vertical distribution of the eggs of *T. trachurus*. Kiliachenkova (1970) found them abundant at the surface. The eggs of the related *T. symmetricus* in the California Current are most common at the surface but fairly abundant down to 30 m, with smaller numbers occurring deeper (Ahlstrom 1959). We, therefore, assume our eggs came mostly from the top 30 m. *Trachurus trachurus* eggs

hatch 3 or 4 days after being spawned at temperatures from 15° to 19°C (Letaconnoux 1951), so average age in our material should be 1.5 to 2 days. Then, taking mean v as 10 cm/s we estimate that a *Trachurus* egg collected near the shelf edge was probably spawned near the edge about 7 to 10 miles farther north.

Maurolicus eggs (Figure 5E) were most abundant just outside the shelf edge. Adults are mesopelagic fish of the continental slope (Maurin et al. 1970; Hureau and Tortonese 1973) and presumably spawn there. We frequently found eggs on the outer one-third of the shelf as well as on the slope, which suggests some eastward transport. The current meter data from arrays 3 and 4 show a mean u about 10 cm/s to the east at 60 m. This could account for the observed distribution if *Maurolicus* eggs occur at that depth and hatch in a few days. Eggs of *M. japonicus* off Japan are most abundant at 50 to 60 m (Nishimura 1957). This species is considered synonymous with *M. muelleri* (Hureau and Tortonese 1973).

Clupeoid larvae (Figure 5F) were abundant at midshelf, on the outer shelf, and over the slope. In general their distribution extended about 10 to 15 miles west of the eggs. Their average age probably was 10 to 20 days more than that of the eggs. Larvae of *Sardina pilchardus* and *Engraulis encrasicholus* occur most commonly in the upper 25 m (Fage 1920). Thus the movement of 20-m shelf water towards the west at about 0.9 nautical mile/day generally explains the observed larval distribution. This water movement is presumably the Ekman transport, which provides a mechanism for the coastal upwelling.

Larvae of demersal fish (flatfish and sparids) occurred mostly on the shelf as expected, but occasionally on the slope. They were most common in inshore waters where eggs and larvae of pelagic species were scarce (Figure 5G, H).

VERIFICATION FROM COMMERCIAL FISH CATCHES

From egg and larval evidence, the adult pelagic fishes in the area and period of JOINT-I should have been predominantly *S. pilchardus* and *E. encrasicholus*, especially the former, on the shelf; *Trachurus*, probably *T. trachurus*, at the shelf edge; and the mesopelagic *M. muelleri*, on the continental slope. Differences in fecundity between species could affect these findings, however, and other species could have been present but not spawning. Commercial fish catches provide a useful check on the results of the studies with eggs and larvae. Some useful information of that type was kindly provided by the Sea Fisheries Institute of Gdynia, Poland.

Polish pelagic (mid-water) trawlers of the Odra Deep Sea Fishing Company fished just south of the JOINT-I area at the end of March 1974. They operated from lat. 20°40′ to 21°00′N, between the coast and shelf edge. Reported catches (tons/day) of pelagic species were about 3.3 *Trachurus* spp., 6.5 *Caranx rhonchus*, and 0.2 *Scomber japonicus*. *Caranx rhonchus* was the principal species within the 50-m isobath, *Trachurus* the principal fish in more offshore waters. During April, the trawlers were located far north of the JOINT-I area between lat. 23° and 27° N, where their catches were predominantly *Sardina pilchardus*.

The Polish research vessel *Professor Siedlecki*, equipped for large-scale pelagic trawling, made 77 hauls between 13 May and 24 June, starting just after JOINT-I. The hauls were made between lat. 20°16′ and 25°01′N which includes the area of JOINT-I. Hauls north of lat. 21°00′ were all on the continental shelf between the 35- and 70-m isobaths and caught almost exclusively *Sardina*. Hauls south of lat. 21°00′ were made at the shelf edge (100-m isobath) and caught almost exclusively *Trachurus* or *Sardina*, usually *Trachurus*.

Klimaj (1971, 1973) summarized results of commercial Polish trawling from 1965 to 1971 in a small area (his area 22) which includes the area of JOINT-I. The principal pelagic fishes taken from March to May were *Trachurus* spp., *Caranx rhonchus*, *Scomber japonicus*, and *Pomatomus saltatrix*. *Caranx rhonchus* was common only in March and *P. saltatrix* only in May. The other two were important in all months, with *Trachurus* generally much more abundant than *Scomber*. The *Trachurus* would have been either *T. trachurus* or *T. trecae*, which are not distinguished in the Polish fishery.

It was noted earlier that the principal spawning seasons of *Caranx* and *Scomber* are respectively later and earlier than the period of JOINT-I. The spawning season of *Pomatomus* is also later (references in Blackburn 1975). Thus these forms could have occurred in the area and period of JOINT-I although we did not recognize them in the ichthyoplankton. *Caranx rhonchus* probably did occur in March, especially inshore, and *S. japonicus* may have occurred, although not in great abundance.

The Polish data support our conclusion that *Trachurus* was the principal pelagic fish at the edge of the shelf. Our conclusion that *Sardina pilchardus* was an important species on the shelf is supported by the results of the *Professor Siedlecki* hauls, but not by those from the commercial vessels. Commercial fishing for that species is concentrated farther north, especially between lat. 24° and 26°N (Chabanne and Elwertowski 1973; Odra Company results given above). Sardine catches of the *Professor Siedlecki* were much higher between lat. 22° and 25°N (mean of 62 hauls, 2.37 tons/h) than between lat. 20° and 22°N (mean of 15 hauls, 0.17 ton/h). There appears to be no commercial fishing for *Engraulis* off Spanish Sahara.

SPATIAL AND TEMPORAL DISTRIBUTION OF SARDINE AND ANCHOVY EGGS

In this section we characterize the area in which sardine and anchovy eggs occurred on JOINT-I, and note temporal changes in their abundance. The findings on areal distribution would apply also to adult fish in reproductive condition. We have assembled data on temperature, chlorophyll *a*, small zooplankton (<500 μm), large zooplankton (>500 μm), sardine eggs, and anchovy eggs for the 10 series along lat. 21°40′N. Figures 2 to 4 show the data for three series, including the two series in which sardine eggs were most abundant. Anchovy eggs were most abundant in the 23-24 March series (Figure 2).

Vertical distributions of temperature and density varied as shown by Barton (1974) and L. A. Codispoti (pers. commun.), and are not discussed in detail. Figure 3 shows typical coastal upwelling and Figure 4 a relaxation of upwelling conditions. Figure 2 shows weak coastal upwelling and upwelling at the shelf edge. Other series showed similar variations. It is doubtful if upwelling ever occurred only at the edge.

Chlorophyll *a* in the water column always showed a primary or secondary maximum on the middle or outer part of the shelf, and sometimes another maximum over the slope. The maximum over the slope was found when upwelling occurred at the edge, as in Figure 2, and was probably a result of it. Maxima of small zooplankton were distributed like those of chlorophyll. Both chlorophyll and small zooplankton were relatively low, close inshore in all series, and also beyond the shelf edge in series where second maxima did not occur. Large zooplankton were relatively scarce on the shelf in each series. Their biomass increased sharply at the edge, and generally continued high as far offshore as we sampled.

Sardine and anchovy eggs were virtually confined to the middle and outer parts of the shelf on all series, regardless of their abundance. Their mean abundance there is given in Table 1, together with means of temperature, chlorophyll, and small zooplankton for the water column in the same area, for each series. Temperature means are approximate.

DISCUSSION

Sardine eggs were most abundant on the middle and outer continental shelf during haul series 5 and 10, moderately abundant during series 8, and scarce on other series (Table 1). Figures 2 to 4 show the abundance on series 5, 9, and 10. Low numbers of eggs indicate either a small population of adults in the vicinity, or one that is spawning little. Mean biomass of adult fish was estimated acoustically for the same part of the shelf on the same sampling line, at various dates commencing 31 March (Thorne et al. in press). This biomass showed an irregular increase with time. It was about 8 g/m^2 on 31 March, 40 g/m^2 on 6 to 9 April and 22 to 26 April, and 80 g/m^2 on 1 to 6 May. These four periods were close in time to series 6, 7, 9, and 10, respectively. The predominant species was probably sardine as stated earlier. The egg numbers show that adult sardines were probably abundant on series 5 and moderately so on series 8, but we have no acoustic estimates of biomass for those series or for series 1 to 4.

The low mean egg number on series 6 probably reflected a very small adult population, but it is unlikely that the low numbers on series 7 and 9 did so, in view of the biomass estimates just given. It is more probable that sardine spawning was inhibited during series 7 and 9. The low mean temperatures in the water column during those series, namely, 15.5° and 16.0°C (Table 1), could have been responsible. Furnestin and Furnestin (1959, 1970) stated that spawning of *Sardina* is absent or feeble below 15.5°C and optimal from 16.0° to 18.0°C, especially over 16.5°C, in Moroccan waters. Spawning might, therefore, be low at 15.5° to 16.0°C in waters off Spanish Sahara. The limiting effect of temperature appears to be not on the spawned eggs, which can develop at 10°C

(Larrañeta 1960), but on the adults, as to whether or not they release eggs. The adults occur in most parts of the water column (Furnestin and Furnestin 1970; Thorne et al. in press), which is the reason for considering mean water temperature here. Furnestin and Furnestin (1970) make it clear that spawning depends on the temperatures over most of the water column, not necessarily on those in the upper 25 m where most eggs are found. Thick layers of water below 15.5°C make an area unsuitable for sardine spawning even if there is warm water at the surface, according to those authors. Figure 3 shows such a situation for series 9. From the criteria of Furnestin and Furnestin and the vertical distributions of temperature in our 10 series (examples given in Figures 2-4), it can be said that temperature conditions on series 3, 4, 7, and 9 were unsuitable for sardine spawning on the middle and outer shelf. Conditions on the other series were relatively suitable with mean temperatures for the water column at 16.5° or 17.0°C. It can then be deduced that adult sardines were scarce on series 1 and 2, because few eggs were found. We have no information about relative abundance of adults on series 3 and 4; they could have been present but not spawning. Relative abundance of adult sardines on the other series is given as low, medium, or high in Table 1, according to indications discussed above.

This succession of changes in abundance of adults is too irregular to be attributed to growth of individuals in a stationary population. It must be due largely to movements into and out of the small area studied. In the last major change, the biomass approximately doubled in about 2 wk between series 9 and 10. No pelagic fish species has such a high growth rate for adult individuals. It was noted during April and May that fish on the continental shelf were more abundant north of the sampling line (as far as lat. 22°20′N, which was the limit of the acoustic surveys) than along the sampling line (Thorne et al. in press). The fishing results of the *Professor Siedlecki* also indicated that sardines were more abundant to the north of our area than within it. It is therefore very probable that the biomass increase between series 9 and 10 represented a movement of sardines into the study area from the north.

It is of interest to consider possible causes of the sardine movements. A population of sardines living off the southern part of the coast of Spanish Sahara would be likely to move into a particular area, like our study area, when conditions were suitable to them and move out of the area when conditions became unsuitable. The principal determinants of distribution of pelagic fish are believed to be temperature and food supply. Temperature conditions in the study area were suitable for adult sardines during the whole period of JOINT-I, since they occur in waters from 14° to 18°C off Morocco (Furnestin and Furnestin 1970). Changes in abundance of food might however have caused movements of sardines into and out of the study area. No studies of the diet of *Sardina pilchardus* have been made off Spanish Sahara except for two fish mentioned later. Elsewhere in its range, including waters off Morocco, it feeds on phytoplankton and small zooplankton (Larrañeta 1960; Furnestin and Furnestin 1970). The distribution of sardines along the sampling line was like that of phytoplankton and small zooplankton as shown earlier: all three having maxima on the middle and outer parts of the continental shelf. This suggests that relative abundance of one or both of those kinds of food determines sardine distribution in a spatial sense and might do so in a temporal sense.

Comparison of means of zooplankton concentration with data on sardine abundance (Table 1) shows no relation between them. If means of chlorophyll concentration are used, there is the following relation: sardine abundance is low when chlorophyll values are 115 mg/m^2 or less, and medium or high when chlorophyll values are 147 mg/m^2 or more. This suggests that sardines entered the study area in order to feed on phytoplankton when it was relatively abundant and left the area when phytoplankton was relatively scarce.

No adult sardines were obtained during JOINT-I. On cruise AUFTRIEB 1975 we caught two sardines in the same area in February. M. Elbrächter kindly identified the contents of their stomachs: one contained no organisms except foraminifera, and the other contained phytoplankton in good condition, including 15 species of diatoms, and 2 species of dinoflagellates, and 2 copepods. Thus *S. pilchardus* feeds on phytoplankton and zooplankton off Spanish Sahara, as it does off Morocco and in other parts of its range. Phytoplankton might be an important part of the diet of the Sahara sardine, sufficiently to cause the sardine to move in relation to changes in phytoplankton abundance as suggested by our data, but we cannot be certain. More work on the diet of the sardine off Spanish Sahara is needed. Mauritanian

sardines have more gillrakers than Moroccan sardines of the same size (Furnestin 1955). This could signify that the mean size of organisms in the diet of sardines decreases from north to south along the African coast.

Table 1 shows that abundance of anchovy (*Engraulis*) eggs does not run parallel in time with that of sardine eggs. There is a large difference between the ratio of the mean numbers of the two kinds of eggs on series 5 and 10, for instance, although temperatures were about the same (Figures 2, 4). We are unable to draw any conclusions about changes in anchovy abundance and their causes, even in the tentative ways attempted here for the sardine.

The concentration of *Trachurus* at the shelf edge may indicate a feeding aggregation on large zooplankton, such as euphausiids and large copepods, which are more abundant there than on the shelf (Figures 2-4). The high abundance of large zooplankton sometimes extends farther offshore than *Trachurus*, however. Some other factor must help to determine abundance of *Trachurus*. The diet of *T. trachurus* and *T. trecae* off northwest Africa is about 80% euphausiids, 10% copepods, and 10% small fish such as anchovy (Boely et al. 1973). Phytoplankton is sometimes a minor constituent of *Trachurus* stomach contents, however (Letaconnoux 1951; Overko 1964; S. Schulz pers. commun.).

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LITERATURE CITED

ABOUSSOUAN, A.
1967. Oeufs et larves de teleosteens de l'ouest africain. 5. *Caranx rhonchus* Geoffr. St.-Hil. (Carangidae). Affinites avec *Trachurus trecae* Cadenat. Bull. Inst. Fondam. Afr. Noire, Ser. A, Sci. Nat. 29:1039-1050.

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.

BARTON, D.
1974. Upwelling events during JOINT I. CUEA (Coastal Upwelling Ecosystems Anal.) Newsl. 3(5):21-27.

BLACKBURN, M.
1975. Summary of existing information on nekton of Spanish Sahara and adjacent regions, northwest Africa. CUEA (Coastal Upwelling Ecosystem Anal.) Tech. Rep. 8, 49 p.

BOELY, T., A. WYSOKINSKI, AND J. ELWERTOWSKI.
1973. Les chinchards des côtes sénégalaises et mauritaniennes. Doc. Sci. Provis., O.R.S.T.O.M., Dakar, 46, 47 p.

BRAVO DE LAGUNA CABRERA, J., AND E. SANTAELLA ALVAREZ.
1973. Observaciones biológico-pesqueras en el banco pesquero sahariano. Bol. Inst. Esp. Oceanogr. 171, 79 p.

CHABANNE, J., AND J. ELWERTOWSKI.
1973. Cartes des rendements de la pêche des poissons pélagiques sur le plateau continental nord-ouest africain de 11°à 26°N. Doc. Sci. Provis., O.R.S.T.O.M., Dakar, 49, 8 p.

CONAND, F., AND E. FAGETTI.
1971. Description et distribution saisonièrre des larves de sardinelles des côtes du Sénégal et de la Gambie en 1968 et 1969. Cah. O.R.S.T.O.M., Sér. Océanogr. 9:293-318.

CONAND, F., AND C. FRANQUEVILLE.
1973. Identification et distribution saisonièrre de larves de carangidés au large du Sénégal et de la Gambie. Bull. Inst. Fondam. Afr. Noire 35, Ser. A, Sci. Nat. 4:951-978.

CUSHING, D. H., G. F. HUMPHREY, K. BANSE, AND T. LAEVASTU.
1958. Report of the committee on terms and equivalents. Cons. Perm. Int. Explor. Mer Rapp. P.-V. Réun. 144:15-16.

DE BUEN, F.
1931. Clupéidés et leur pêche (4e rapport). Rapp. P.-V. Réun. Comm. Int. Explor. Mer Méditerr. 6:289-336.
1937. Clupéidés et leur pêche (7e rapport). Rapp. P.-V. Réun. Comm. Int. Explor. Mer Méditerr. 10:317-419.

DEMIR, N.
1963. Synopsis of biological data on anchovy *Engraulis encrasicolus* (Linnaeus) 1758 (Mediterranean and adjacent seas). FAO Fish. Synop. 26, 44 p.

FAGE, L.
1920. Engraulidae, Clupeidae. Rep. Dan. Oceanogr. Exped. 1908-1910, Mediterr. 2, Biol. A9, 140 p.

FURNESTIN, J.
1955. Remarques sur quelques caractères de la sardine de Mauritanie (*Sardina pilchardus* Walbaum). Cons. Perm. Int. Explor. Mer Rapp. P.-V. Réun. 137:24-25.

FURNESTIN, J., AND M. L. FURNESTIN.
1959. La reproduction de la sardine et de l'anchois des côtes atlantiques du Maroc (Saisons et aires de ponte). Rev. Trav. Inst. Pêches Marit. 23:79-104.
1970. La sardine marocaine et sa pêche. Migrations trophiques et génétiques en relation avec l'hydrologie et le plancton. Cons. Perm. Int. Explor. Mer Rapp. P.-V. Réun. 159:165-175.

HUREAU, J. C., AND E. TORTONESE.
1973. Carangidae. *In* J. C. Hureau and Th. Monod (editors), Check-list of the fishes of the north-eastern Atlantic and of the Mediterranean, Clofnam I, p. 373-384. Unesco, Paris.

KILIACHENKOVA, V. A.
1970. Development and distribution of eggs and larvae of *Trachurus trachurus* L. Cons. Perm. Int. Explor. Mer Rapp. P.-V. Réun. 159:194-198.

KLIMAJ, A.
1971. Atlas rybacki (Fishery atlas) szelfu Afryki Polnocno-zachodniej. Tom. 1. Morsk. Inst. Rybacki, Gdynia, 129 p.
1973. Atlas rybacki (Fishery atlas) szelfu Afryki Polnocno-zachodniej. Tom. 2. Polowy Pelagiczne. Morsk. Inst. Rybacki, Gdynia, 128 p.

LARRAÑETA, M. G.
1960. Synopsis of biological data on *Sardina pilchardus* of the Mediterranean and adjacent seas. *In* H. Rosa, Jr. and G. Murphy (editors), Proc. World Scientific Meeting on the Biology of Sardines and Related Species, p. 137-173. Food Agric. Organ. U.N., Rome.

LETACONNOUX, R.
1951. Contribution à l'étude des espèces du genre *Trachurus* et spécialement du *Trachurus trachurus* (Linné 1758). Mém. Off. Sci. Tech. Pêches Marit. 15, 67 p.

LORENZEN, C. J.
1968. Carbon/chlorophyll relationships in an upwelling area. Limnol. Oceanogr. 13:202-204.

LOZANO CABO, F.
1970. Caractéristiques zoogéographiques de la faune ichthyologique des côtes des îles Canaries, du Maroc, du Sahara espagnol et de la Mauritanie avec une étude speciale des poissons côtiers. Cons. Perm. Int. Explor. Mer Rapp. P.-V. Réun. 159:152-164.

MAIGRET, J.
1972. Campagne experimentale de pêche des sardinelles et autres espèces pélagiques, Juillet 1970-Octobre 1971. Tome 1. Observations concernant l'océanographie et la biologie des espèces. S.C.E.T.-International, 148 p.

MARCHAL, E. G.
1966. Oeufs, larves et post-larves de l'anchois de Golfe de Guinee, *Anchoviella guineensis* (Blache et Rossignol). Doc. Sci. Provis., O.R.S.T.O.M., Abidjan 5, 15 p.
1967. Cle provisoire de determination des oeufs et larves des clupeides et engraulides ouest-africains. Doc. Sci. Provis., O.R.S.T.O.M., Abidjan 14, 10 p.

MAURIN, C.
1968. Ecologie ichthyologique des fonds chalutables atlantiques (de la baie ibéro-marocaine a la Mauritanie) et de la Méditerranée occidentale. Rev. Trav. Inst. Pêches. Marit. 32:1-147.

MAURIN, C., F. LOZANO CABO, AND M. BONNET.
1970. Inventaire faunistique des principales espèces ichthyologiques frequentant les cotes nord-ouest africaines. Cons. Perm. Int. Explor. Mer Rapp. P.-V. Réun. 159:15-21.

NISHIMURA, S.
1957. Vertical distribution of the floating eggs of *Maurolicus japonicus* Ishikawa, a gonostomatid fish, in the sea. Rep. Jap. Sea Reg. Fish. Res. Lab. 3:13-22.

OVERKO, S. M.
1964. Biology and fishing of scad near the northwestern shores of Africa. [In Russ.] Tr. Atl. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 11:45-64.

PILLSBURY, R. D., J. S. BOTTERO, R. E. STILL, AND E. MITTELSTAEDT.
1974. A compilation of observations from moored current meters. Vol. VIII. Wind, currents and temperature off northwest Africa along 21°40'N during JOINT-I, February-April 1974. Sch. Oceanogr. Oreg. State Univ., Data Rep. 62, Ref. 74-20, 143 p.

SAVILLE, A.
1964. Clupeoidae. Cons. Perm. Int. Explor. Mer, Fiches Identification Oeux Larves Poissons 1, 5 p.

THORNE, R. E., O. A. MATHISEN, R. J. TRUMBLE, AND M. BLACKBURN.
In press. Distribution and abundance of pelagic fish off Spanish Sahara during CUEA Expedition JOINT-I. Deep-Sea Res.

UNESCO.
1966. Determination of photosynthetic pigments in seawater. Monogr. Oceanogr. Methodol. 1, 69 p.

VOITURIEZ, B., P. DUFOUR, AND R. LE BORGNE.
1974. Preliminary results on R. V. *CAPRICORNE* 7402 Cruise in Cape Blanc. CUEA (Coastal Upwelling Ecosystem Anal.) Newsl. 3(5):1-7.

WITZELL, W. N.
1973. Gonostomatidae. *In* J. C. Hureau and Th. Monod (editors), Check-list of the fishes of the north-eastern Atlantic and of the Mediterranean, Clofnam I, p. 144-122. Unesco, Paris.

LIFE HISTORY OF COHO SALMON, *ONCORHYNCHUS KISUTCH*, IN SASHIN CREEK, SOUTHEASTERN ALASKA

RICHARD A. CRONE[1] AND CARL E. BOND[2]

ABSTRACT

The freshwater life of coho salmon, *Oncorhynchus kisutch*, in Sashin Creek, southeastern Alaska, was studied from the fall of 1963 through the summer of 1968. Additional information on age composition and fecundity of adults returning to Sashin Creek and a nearby stream was collected through the fall of 1972. Some pre-1963 data on coho salmon entering and leaving Sashin Creek were used. Weir counts and estimates of numbers of adult salmon determined from spawning ground counts and mean redd life were poor measures of the total escapement of coho salmon in Sashin Creek; an estimate made from tagging a portion of the escapement and subsequently determining tagged-to-untagged ratios of spawners on the riffles proved to be a more reliable measure. The number of spawning coho salmon varied for the years 1963 through 1967 from 162 to 916; the dominant age group was 4_3. The salinity of the surface water of the estuary of Sashin Creek usually is less than 10-15‰; bioassays of salinity tolerance indicated that coho salmon fry can survive in these salinities. In 1964, 44,000 coho salmon fry migrated to the estuary soon after emergence, although none of the scales collected from returning spawners in subsequent years showed less than 1 yr of freshwater residence. Survival curves constructed from periodic estimates of the stream populations of juvenile coho salmon for the years 1964-67 showed that mortality was highest in midsummer of the first year of life, when 62% to 78% of the juveniles were lost in a 1-mo period. Most coho salmon smolts migrated from Sashin Creek in late May or early June. In the spring of 1968, 1,440 smolts left Sashin Creek—37% were yearlings, 59% were 2-yr-olds, and 4% were 3-yr-olds. The average fork lengths were 83 mm for yearlings, 105 mm for 2-yr-olds, and 104 mm for 3-yr-olds.

Coho salmon, *Oncorhynchus kisutch* (Walbaum), occur over a broad geographic range in the North Pacific Ocean and Bering Sea. They spawn in coastal streams from northern California to northwestern Alaska and from northern Hokkaido, Japan, to the Anadyr River, USSR (Figure 1). The young usually remain in fresh water for 1 to 3 yr before migrating to sea as smolts; they are sexually mature after about 14 to 18 mo in the sea. In some systems some fry emigrate to salt water in their first spring or summer of life, but they apparently do not contribute significantly to the adult return (Chamberlain 1907; Gilbert 1913; Pritchard 1940; Wickett 1951; Foerster 1955).

Among the numerous populations of coho salmon, there are differences in freshwater life history that appear to be related to latitude. In the southern one-third of their range, coho salmon typically remain in fresh water about 1 yr before they migrate to sea in their second year of life—15 to 18 mo from egg deposition (Pritchard 1940; Briggs 1953; Smoker 1953). Farther north, in Alaska, coho salmon remain 1, 2, or 3 yr (occasionally 4) in fresh water after they emerge from the gravel (International North Pacific Fisheries Commission 1962; Godfrey 1965; Drucker 1972). In some of the Alaska streams and in Kamchatka, USSR, coho salmon that remain in fresh water for 2 yr may represent a larger percentage of the population than those that remain for 1 yr (Gilbert 1922; Semko 1954; Andrews 1962; Logan 1963; Engel 1966; Kubik 1967; Redick 1968; Armstrong 1970; Drucker 1972).

Most studies of coho salmon behavior and survival in fresh water have been conducted in the southern and central parts of the range: California, Oregon, Washington, and British Columbia in the eastern Pacific (Neave 1948; Wickett 1951; Briggs 1953; Smoker 1953; Shapovalov and Taft 1954; Foerster 1955; Salo and Bayliff 1958; Chapman 1962, 1965; Koski 1966); and Kamchatka in the western Pacific (Kuznetsov 1928; Gribanov 1948; Semko 1954). Information on more northerly stocks is much less detailed.

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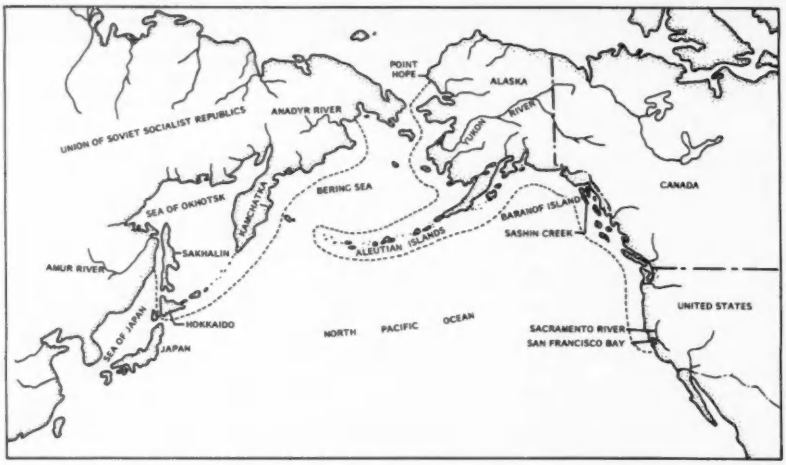

FIGURE 1.—Geographic range of coho salmon in North Pacific Ocean and Bering Sea. Dashed line indicates coastline where coho salmon enter streams for spawning.

In our studies at Sashin Creek, southeastern Alaska, we have attempted to determine important aspects of the life histories of populations of the coho salmon near the center of its range (southeastern Alaska). We have compared our findings with life histories of populations in other parts of the range and have emphasized 1) characteristics of adult spawners (including time of stream entry and time of spawning, longevity on the spawning grounds, age structure, and fecundity), 2) survival of eggs and alevins in the gravel, and 3) survival and growth of juveniles up to the time of seaward migration.

STUDY AREAS

Sashin Creek empties into Chatham Strait in the inner bay of Little Port Walter on the southeastern shore of Baranof Island (Figure 2). The stream originates in Sashin Lake about 3 km from tidewater and drains about 10 km^2 of forested watershed—mostly western hemlock, *Tsuga heterophylla*, and Sitka spruce, *Picea sitchensis* (U.S. Geological Survey 1972).

The discharge pattern of Sashin Creek is governed by seasonal rainfall and the rate of melting of accumulated snow. For the 10-yr period 1963-72, annual precipitation at Little Port Walter averaged about 587 cm (231 inches).[3] Although Sashin Lake intercepts part of the runoff and tends to even out flows in Sashin Creek, discharge varies from less than 0.3 m^3/s in midwinter to as much as 34 m^3/s after heavy rains in September and October.

Salmon have access to the 1,100 m of stream between the weir at the upper limits of salt water and a high waterfall upstream. Coho salmon rarely spawn in the 160 m of stream immediately below the waterfall or in the intertidal stream channel; both areas have a steep gradient and coarse bottom material.

The spawning ground is divided into three areas (upper, middle, and lower) which have different physical characteristics but in total contain about 13,000 m^2 of spawning gravels (Table 1). The upper area contains about 25% of the stream's suitable spawning gravels and is characterized by a steep gradient (relative to the other sections) and coarse bottom materials. The middle area has about 30% of the spawning gravel and an intermediate gradient with a higher proportion of smaller gravel and fines. The lower area is the largest and contains about 45% of the spawning gravel; it has a low gradient and a high proportion of fines in the bottom materials.

Rearing areas of juvenile coho salmon include the three spawning areas plus pools, backwaters, and to a limited extent, the 160-m section of stream in the canyon immediately downstream from the waterfall. In our investigation of juvenile coho salmon, the three ecologically distinct study areas were maintained. An additional 3,473 m^2 were included in the study areas to incorporate

[3]This average was computed from data from volumes 49-58 of the U.S. Weather Bureau's "Climatological Data, Alaska, Annual Summary." However, because precipitation for August 1967 (vol. 53) was reported incorrectly as 6.99 inches, we used the figure from the original records at Little Port Walter of 19.08 inches for August 1967 in computing the 10-yr average precipitation.

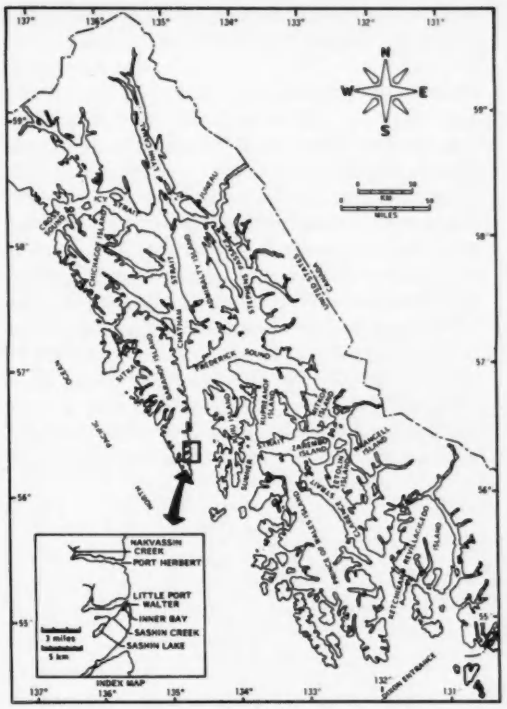

FIGURE 2.–Southeastern Alaska and Little Port Walter region, site of coho salmon study.

pools and backwaters, for a total of 16,557 m^2 (Table 1).

In 1965-67, part of Funny Creek, a small tributary of Sashin Creek near tidewater, was added to the study area. Funny Creek is about 1.5 m wide on the average and slow flowing; the bottom is mostly mud and detritus but has a few gravel areas that are used by coho salmon for spawning. The Funny Creek study area included 441 m^2 of stream from its junction with Sashin Creek upstream 290 m; the first 215 m flows through a muskeg meadow and the most upstream 75 m flows through forest.

The fish fauna of Sashin Creek consists of pink salmon, *O. gorbuscha*; coho salmon; chum salmon, *O. keta*; rainbow trout, *Salmo gairdneri*; Dolly Varden, *Salvelinus malma*; and coastrange sculpin, *Cottus aleuticus*. A few adult sockeye salmon, *O. nerka*, occasionally stray into the stream.

ADULT COHO SALMON STUDIES

In our studies of adult coho salmon we determined: 1) size of escapement, i.e., the number of coho salmon spawners that returned to Sashin Creek; 2) average redd life of females; 3) distribution and density of spawners in each study section; 4) interspecific competition between coho and pink salmon; 5) age structure of spawners; 6) fecundity of females; and 7) egg retention of spent females. In addition, for comparison with data from Sashin Creek, we obtained data on the age and fecundity of adult coho salmon from Nakvassin Creek in Port Herbert, a 7-km-long fiord about 5 km north of Little Port Walter (Figure 2). Nakvassin Creek, about 0.4 km long, is the outlet stream from 30-hectare Nakvassin Lake. Coho and sockeye salmon, Dolly Varden, rainbow trout, coastrange sculpin, and threespine stickleback, *Gasterosteus aculeatus*, inhabit the lake. These species plus pink and chum salmon inhabit Nakvassin Creek.

Size of Escapement

Adult coho salmon generally enter Sashin Creek from early August to early November, but the greatest numbers enter from late August to mid-October. Spawning usually begins early in October and ends in mid-November.

Adult salmon have been counted in Sashin Creek since 1934 through a weir at the head of tidewater. From 1934 to 1969, counts of coho salmon at the

TABLE 1.–Surface area, average gradient, and size composition of bottom materials less than 15.2 cm in diameter in three study areas of Sashin Creek.[1]

Study area	Spawning area (m^2)	Total area[2] (m^2)	Average gradient (%)	Percentage of spawning area composed of: Cobbles (>12.7 mm)	Pebbles and granules (1.68-12.7 mm)	Sands and silts (<1.68 mm)
Upper	2,945	4,049	0.7	81	16	3
Middle	4,067	4,441	0.3	61	26	13
Lower	6,072	8,067	0.1	47	36	17
Total	13,084	16,557	0.3	—	—	—

[1]Table adapted from McNeil (1966).
[2]This area includes pools and backwaters.

weir ranged from 0 to 567 (Table 2). The weir counts are not accurate measures of the number of coho salmon in the escapements, however, because the weir was maintained primarily to count pink salmon and the panels were usually removed at the end of the pink salmon run near the end of September. Moreover, coho salmon can jump over the weir panels and many did so each year and were therefore not counted.

Because of the problems with weir counts, an effort was made to obtain accurate estimates of the coho salmon escapements in 1963-65 and 1967 on the basis of repeated observations of the number and distribution of salmon in the three study areas (Table 3). Adults on the spawning riffles were counted by periodic visual censuses, and the counts were recorded separately for each area. In 1963 and 1964, salmon were counted only when water conditions were most favorable for observing fish; spawners were not recorded separately by sex. In 1965 and 1967, visual surveys were conducted daily, except for 6 days in 1965 when the water was too high to make observations; males and females were recorded separately. Funny Creek was included in the surveys in 1965 and 1967.

Spawners on the riffle areas were usually counted between 1000 and 1400 h, when light conditions were most favorable for observing fish. The observer (wearing polarizing glasses to reduce glare at the water surface) began counting at the upstream end of the spawning area and continued downstream. In 1965 and 1967, the observer recorded the location of individual females with reference to section markers spaced at 30.5-m intervals and a baseline running longitudinally between markers in the stream. The number of

TABLE 2.–Number of adult coho salmon counted into Sashin Creek at the weir by 2-wk intervals, 1934-69.[1]

	Two-week period							
Year	1-14 Aug.	15-28 Aug.	29 Aug.-11 Sept.	12-25 Sept.	26 Sept.-9 Oct.	10-23 Oct.	24 Oct.-7 Nov.	Total
1934	—	—	—	[2]1	—	—	—	1
1935	—	—	—	(2)	—	—	—	0
1936	—	2	2	[2]36	—	—	—	40
1937	—	3	[2]5	—	—	—	—	8
1938	—	—	1	(2)	—	—	—	1
1939	—	16	94	12	(2)	—	—	122
1940	—	—	—	[2]1	—	—	—	1
1941	—	—	—	[2]1	—	—	—	1
1942	—	—	—	[2]2	—	—	—	2
1943	—	5	2	9	[2]12	—	—	28
1944	—	6	1	10	249	[2]62	—	328
1945	—	—	18	98	219	[2]232	—	567
1946	—	—	1	82	6	[2]22	—	111
1947	—	—	21	40	[2]50	—	—	111
1948	—	9	36	19	138	[2]6	—	208
1949	—	—	27	170	[2]5	—	—	202
1950	—	19	7	37	[2]3	—	—	66
1951	1	21	50	10	[2]53	—	—	135
1952	—	20	24	138	30	(2)	—	212
1953	4	3	65	8	[2]35	—	—	115
1954	—	—	46	108	(2)	—	—	154
1955	4	6	74	74	[2]10	—	—	168
1956	—	—	12	73	3	(2)	—	88
1957	—	6	28	—	[2]36	—	—	70
1958	—	16	79	65	[2]19	—	—	179
1959	5	5	33	37	58	[2]133	—	271
1960	—	27	57	19	5	1	(2)	109
1961	51	27	11	5	4	(2)	—	98
1962	—	2	3	29	3	(2)	—	37
1963	—	2	202	[2]107	—	—	—	311
1964	—	10	13	—	(2)	—	—	23
1965	—	—	100	1	[2]23	—	—	124
1966	—	—	82	[2]8	—	—	—	90
1967	—	30	49	[2]4	—	—	—	83
1968	—	14	100	[2]70	—	—	—	184
1969	4	—	3	(2)	—	—	—	7
Total	69	249	1,246	1,274	961	456	—	4,255
Percent of all fish counted	1.6	5.9	29.3	29.9	22.6	10.7	—	—

[1]Daily counts for 1934-63 from Olson and McNeil (1967).
[2]Weir discontinued during this period.

males near each female and the number of males on the riffles but not with females also were recorded.

The estimates of the total number of spawners based on the periodic counts on the spawning riffles were obtained in the following manner. The counts of both sexes were plotted against time (Figure 3). In the figure each point for 1965 and 1967 represents the average of three successive daily counts of spawners, and each point for 1963 and 1964 represents a daily count. A curve was drawn by eye through each set of points, and the resulting area under the curve represents the spawning effort in fish-days (see Table 3 and section on Redd Life). The estimates of the total number of spawners were then derived by dividing the total number of fish-days by the average redd life (the number of days a female spends on the spawning site or redd). The method was modified from McNeil (1966). The average of the mean redd life computed for coho salmon females in 1965 and 1967 was used to calculate total number of spawners in 1963 and 1964.

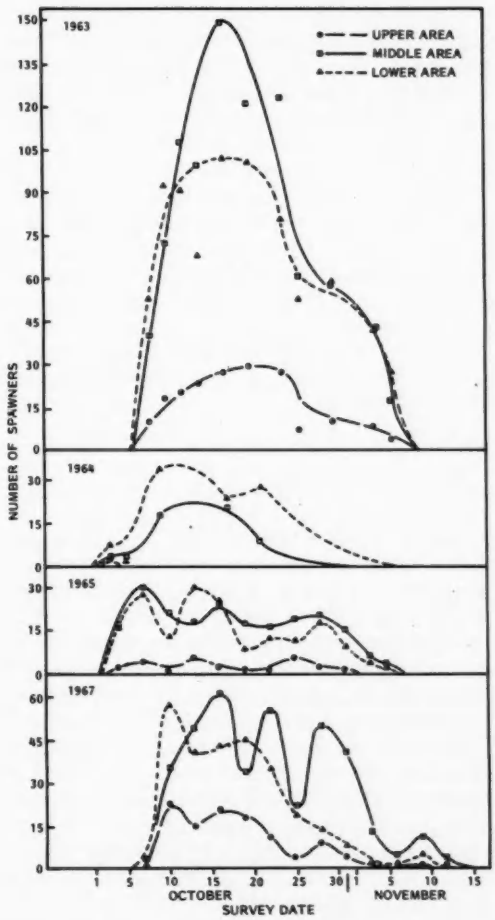

FIGURE 3.–Stream survey estimates of numbers of spawning coho salmon in Sashin Creek, based on periodic counts on spawning riffles, 1963-65 and 1967. Area under each curve is spawning effort, expressed in fish-days.

As indicated in the following tabulation, estimates of the total number of spawners derived from the stream survey data were much higher than the counts at the weir, except for 1965.

Year	*Counted at weir*	*Derived from stream survey (spawning effort-redd life)*
1963	311	458
1964	23	81
1965	124	94
1967	83	209

We also estimated the size of the escapement in 1965 and 1967 by conducting a mark-recapture experiment using the Bailey modification of the Petersen formula as given by Ricker (1958). In 1965, 46 adult coho salmon (32 females and 14 males) were tagged before spawning; in 1967, 73 unspawned coho salmon (28 females and 45 males) were tagged. The tags used were plastic Petersen disks. Marked-to-unmarked ratios were obtained from observations made during the visual censuses and these were used to estimate the populations. Based on the marked-to-unmarked ratios, the estimated number of coho salmon spawners (both sexes) in Sashin Creek was 221 in 1965 and 370 in 1967 (Table 4).

The estimates of escapement size in 1965 and 1967 based on marked-to-unmarked ratios were much higher than either the counts at the weir or the estimates based on spawning effort and redd life (Table 4). Several possible sources of error existed in estimating numbers of spawners from spawning effort and redd life: 1) The levels of spawning activity were lower at low streamflows, when visibility was good, and higher at high streamflows (Figure 4), when visibility was restricted. (In other words, the least accurate counts of spawners occurred when the greatest numbers were spawning.) 2) Some redds were occupied only at night (indicated from our limited observations). 3) The assumption that the mean spawning life of females was equal to that of males could be invalid.

TABLE 3.—Distribution and density of spawning coho salmon in three areas of Sashin Creek in 1963-65 and 1967.

Brood year	Distribution: % of total salmon observed			Spawning effort (fish-days)				Density of spawning (fish-days per square meter)			
	Upper area	Middle area	Lower area	Upper area	Middle area	Lower area	Total	Upper area	Middle area	Lower area	Total
1963[1]	10	48	42	553	2,652	2,289	5,494	0.19	0.65	0.38	0.42
1964	1	35	64	5	297	674	976	<0.01	0.07	0.11	0.07
1965	6	51	43	74	607	543	1,224	0.03	0.15	0.09	0.09
1967	14	50	36	320	1,151	828	2,299	0.11	0.28	0.14	0.18

[1]W. J. McNeil, unpublished notes on 1963 coho studies. On file at Auke Bay Fisheries Laboratory, Auke Bay, AK 99821.

TABLE 4.—Estimates of coho salmon escapements to Sashin Creek, 1963-65 and 1967, based on three methods of estimation.

Method of estimation	Number of coho salmon each year: 1963	1964	1965	1967
Weir count	311	23	124	83
Spawning effort and redd life	458	81	94	209
Marked to unmarked ratios	—	—	221	370
(95% confidence interval)	—	—	197-250	342-403
Spawner escapement assumed in this report	[1]916	[1]162	221	370

[1]Based on observations in 1965 and 1967 that spawning ground counts and redd life estimates were about one-half the estimates based on marked-to-unmarked ratios of spawners.

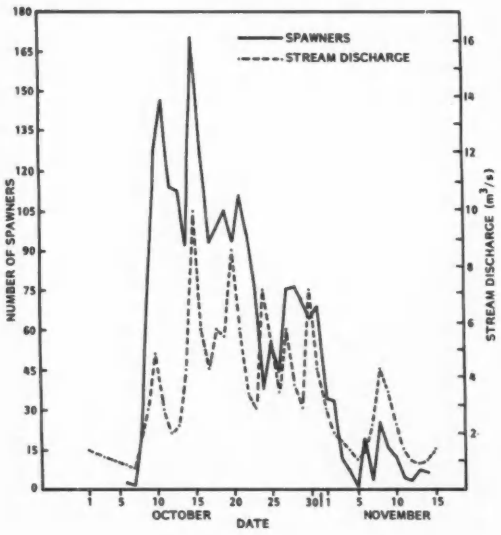

FIGURE 4.—Spawning ground counts of coho salmon in relation to stream discharge, Sashin Creek, 1967.

We believe that the best estimates of abundance of spawners are those based on tagging and observing marked-to-unmarked ratios, but such estimates are not available for 1963 and 1964. Therefore, because the estimates derived from spawning effort and redd life in 1965 and 1967 were approximately one-half the estimate from marked-to-unmarked ratios, the assumption was made that in 1963 and 1964, only 50% of the spawners in Sashin Creek were estimated from spawning effort and redd life. Our best estimates of the numbers of coho salmon spawners are 916 in 1963, 162 in 1964, 221 in 1965, and 370 in 1967 (Table 4). These values are used in the remainder of this report.

The population estimates of coho salmon spawners in Sashin Creek do not include jack coho salmon (precocious males of various freshwater ages but only one summer of marine life) because none were tagged; without tags, their presence on the spawning riffles would have been difficult to detect. Apparently, only a few jack coho salmon enter Sashin Creek; none were seen during the 1965 surveys of the spawning grounds, and only five were seen during underwater observations in 1967.

Redd Life

The estimates of mean redd life used in our calculations of escapement size were based on experiments with marked females in Sashin Creek in 1965 and 1967. Many untagged females that could be identified from natural markings, such as wounds, fungused areas, color, and size, were used along with the tagged females. A female had to be observed at the same location on two consecutive days before she was considered to have selected a permanent spawning site. One day was added to the observed redd life for females, on the assumption that they began to construct a redd an average of one-half day before first being observed and remained on the redd for an average of one-half day after last being observed.

The mean redd life of female coho salmon varied between tagged and untagged (identified from natural markings) females in both 1965 and 1967. In 1965 the mean redd life for 56 females (18

tagged and 38 untagged) was 13 days (range of 6 to 21 days). In 1967, 151 females (21 tagged and 130 untagged) remained an average of 11 days on the spawning riffles (range of 3 to 24 days). Tagged females had shorter mean redd lives than untagged females—12 versus 13 days in 1965 and 9 versus 11 days in 1967. The difference between tagged and untagged fish may have been due to difficulty in positively identifying untagged females with short redd lives, thus biasing the mean toward a greater value. Also, handling and tagging might have resulted in a shorter mean redd life for tagged females.

Tagged male coho salmon in Sashin Creek and both sexes in Funny Creek had shorter spawning lives than tagged females in Sashin Creek. Because males in Sashin Creek in 1965 were all tagged with the same color and could not be recognized individually on the spawning grounds as they moved from female to female, their spawning life could not be calculated. In 1967, however, the males in Sashin Creek had a mean spawning life of 9 days. The spawning life of coho salmon (males and females combined) was from 3 to 7 days in Funny Creek in 1965 and 1967. Rapidly rising and falling water levels, which caused some spawners to leave the area at low flows, and predation by brown bears, *Ursus arctos*, probably contributed to the shorter spawning life in Funny Creek.

In Sashin Creek, stream life and spawning life are not the same length because many coho salmon enter the stream and mature in pools for a month or more before they spawn. In Oregon, the mean length of time that female coho salmon spent in a tributary of Wilson River, Spring Creek, before death was 11 days (Willis 1954). Adults migrating into Spring Creek frequently begin spawning as soon as they enter the tributary; apparently they stay in the larger Wilson River until they are ripe (Willis 1954). Koski (1966) reported mean stream lives of 13.7 and 13.1 days for coho salmon that spawned in two tributaries to Drift Creek, Oreg.

Distribution and Density of Spawners

The distribution and density of spawners on the Sashin Creek spawning grounds were observed in 1963, 1964, 1965, and 1967 (Table 3). Distribution in each study area is expressed as the percentage of the total number of salmon observed spawning and as total spawning effort (fish-days) observed in each area. Density is the observed spawning effort divided by the square meters of spawning area.

In each of the 4 yr, the density of spawning coho salmon was higher in the middle and lower study areas than in the upper. In 1963, 1965, and 1967, the middle area had the highest density of spawners; in 1964 the lower area had the highest.

In Funny Creek a few coho salmon were seen spawning in 1965 and 1967. In those 2 yr about 4% of the estimated escapement of coho salmon to Sashin Creek spawned in Funny Creek.

The distribution and escapement of pink and coho salmon in Sashin Creek are shown in Table 5. Pink salmon usually were distributed more evenly throughout the creek than coho salmon. Merrell (1962) and McNeil (1966) reported that spawning pink salmon used the upper area extensively only in years when spawning escapements were large; when pink salmon escapements were small, spawning was concentrated in the lower area. The fact that relatively few coho salmon used Sashin Creek may explain why such a small proportion spawned in the upper area. In addition, ecological features of that area such as steep gradient and coarse bottom materials may limit its usefulness for spawning.

TABLE 5.—Distribution and escapement of spawning coho and pink salmon in three study areas of Sashin Creek, 1963-67.

Year and species of salmon	Escapement	Percentage of total salmon observed		
		Upper area	Middle area	Lower area
1963				
Coho	916	10	48	42
Pink	16,757	19	41	40
1964				
Coho	162	1	35	64
Pink	2,193	3	30	67
1965				
Coho	221	6	51	43
Pink	14,813	24	39	37
1966				
Coho	(1)	—	—	—
Pink	5,761	4	41	54
1967				
Coho	370	14	50	36
Pink	38,067	27	35	38

[1]The weir count of coho salmon was 90 when the weir gates were removed in md-September.

Interspecific Competition

Pink salmon are the most abundant fish in Sashin Creek—the number of adult pink salmon ranged from about 2,000 to 72,000, and their progeny ranged from about 0.3 to 3.6 million for the years of this study, 1963-72.

Because pink salmon complete their spawning

in Sashin Creek before coho salmon spawning begins, spawning by coho salmon could be detrimental to pink salmon embryos. In 1965, we tried in each of the three study areas to assess the effect of coho salmon superimposing their redds on those of pink salmon. The densities of live pink salmon embryos, which were estimated from routine sampling of the spawning riffles with a hydraulic sampler prior to coho salmon spawning (McNeil 1964), were used in conjunction with the average size of a coho salmon redd to estimate the total number of pink salmon embryos that could have been destroyed in gravel disturbed by spawning coho salmon. At 13 redds throughout the stream the average area of gravel disturbed by spawning coho salmon was 2.6 m^2 per redd.

The possible effect of coho salmon spawning on pink salmon embryos in October 1965 is shown in Table 6. The estimated spawning population of 110 female coho salmon would have disturbed a total of 286 m^2 of spawning gravel. Hydraulic sampling of the spawning grounds in late September before the coho salmon spawned indicated an average density of 680 live pink salmon embryos per square meter (see footnote 1, Table 6). About 200,000 live pink salmon embryos resided in areas disturbed by coho salmon spawners.

In years when the numbers of coho and pink salmon spawners are similar to those of 1965, it is doubtful that coho salmon spawning has a significant detrimental effect on the survival of pink salmon embryos. Even assuming complete mortality of pink salmon embryos in gravels utilized by spawning coho salmon, the impact on survival of pink salmon in 1965 would have been slight–about 2% of the viable pink salmon embryos present. Mortality of pink salmon eggs from redd superimposition by coho salmon could be significant if the number of coho salmon spawners were to greatly increase by natural or artificial processes.

Age Determination

We determined the age structure of samples of adult coho salmon in Sashin Creek in 1965-67 and 1969 and in Nakvassin Creek in 1966-72 by scale analysis (Table 7). Most of the salmon had spent two summers and two winters in fresh water after emergence from the gravel, had migrated to sea in the beginning of their third year, and had then spent two summers and one winter in the ocean (designated in the Gilbert-Rich system as age 4_3). A smaller portion of those sampled had spent 1 yr in fresh water after emergence, had entered the sea at the beginning of their second year, and had then remained two summers in the ocean (age 3_2). Adults that had migrated to sea at the beginning of their fourth year of life and spent two summers in salt water (age 5_4) usually constituted the smallest fraction of each year's run.

The presence of a large and dominant brood year of coho salmon in Nakvassin Creek is indicated by the percentage age distribution of returning adults. In 1967, 40% of the adults sampled for scales were age 3_2–1964 brood coho salmon that had spent 1 yr in fresh water before migrating as smolts; in 1968, 94% of the adults

TABLE 7.–Age structure as determined from samples of scales of adult coho salmon from Sashin Creek, 1965-67 and 1969, and Nakvassin Creek, 1966-72.

Source and year of sample	No. of fish sampled	Percentage age distribution		
		3_2	4_3	5_4
Sashin Creek:				
1965	27	18	78	4
1966	17	29	59	12
1967	76	25	64	11
1969	16	37	62	0
Nakvassin Creek:				
1966	25	28	68	4
1967	20	40	55	5
1968	16	6	94	0
1969	28	11	61	29
1970	46	15	76	9
1971	78	8	88	4
1972	92	9	71	21

TABLE 6.–Possible effect of coho salmon spawning on pink salmon embryos in Sashin Creek steambed in October 1965.

Area	Percentage of observed coho salmon spawning effort	Estimated coho salmon females	Area of gravel disturbed by coho salmon (m^2)	Live pink salmon embryos/m^2 before coho salmon spawned[1]	Estimated viable pink salmon embryos disturbed by coho salmon	Estimated viable pink salmon embryos in study areas	Percentage of total pink salmon embryos disturbed by coho salmon
Upper	6	7	18	750	14,000	2,209,000	0.6
Middle	51	56	146	1,200	175,000	4,880,000	3.6
Lower	43	47	122	300	37,000	1,822,000	2.0
Total	100	110	286	[2]680	226,000	8,911,000	[3]2.2

[1]W. J. McNeil, Auke Bay Fisheries Laboratory, (pers. commun.).
[2]Mean density, weighted according to area size.
[3]Mean percentage, weighted according to area size.

were 4_3–1964 brood coho salmon that had spent 2 yr in fresh water; and in 1969, 29% of the adults were 5_4–1964 brood coho salmon that had spent 3 yr in fresh water. Another large brood year indicated by the ages of returning adults is the 1967 brood. No similar patterns of a strong brood year are evident in the 4 yr of data from Sashin Creek coho salmon (Table 7).

Direct comparison of the many studies on age composition of coho salmon must be done with caution because of year-to-year variations and different sampling techniques, but a general clinal change in freshwater and total age with latitude is suggested–southerly populations are predominantly age 3_2 and northerly populations predominantly age 4_3. In British Columbia, Washington, Oregon, and California, coho salmon (exclusive of jacks) are almost all age 3_2 (Pritchard 1940; Marr 1943; Smoker 1953; Shapovalov and Taft 1954; International North Pacific Fisheries Commission 1962). Gilbert (1922) reported that about 60% of the coho salmon of the Yukon River were age 4_3; the remainder were age 3_2. Coho salmon populations in most streams studied in the Cook Inlet-Kenai Peninsula area of Alaska are composed of 60% to 95% age 4_3 fish (Andrews 1962; Logan 1963; Engel 1966; Kubik 1967; Redick 1968). In the Karluk River system on Kodiak Island, Alaska, age 4_3 fish also are dominant but age 5_4 fish, rather than age 3_2, are the second most abundant (Drucker 1972). Semko (1954) listed age composition of coho salmon from the Bolshaya River, Kamchatka, for 8 yr; in two of the years (1946 and 1947) age 4_3 adults outnumbered age 3_2. The highest percentage of age 4_3 fish reported by Semko (1954) was 64.7%. The age composition of coho salmon from the commercial fisheries of the Taku and Stikine rivers in southeastern Alaska in 1955 was 68.0% age 3_2 and 28.2% age 4_3 (International North Pacific Fisheries Commission 1962). A later report on Stikine River coho salmon caught in 1955 gives age composition as 45.2% age 3_2 and 51.9% age 4_3 (Godfrey 1965). Of several thousand coho salmon represented by scales collected from the commercial fisheries in southeastern Alaska, about half spent one winter in fresh water (age 3_2) and half spent two winters in fresh water (age 4_3) (Smoker 1956). Nearly equal numbers of ages 3_2 and 4_3 also were reported for coho salmon at Hood Bay Creek in southeastern Alaska (Armstrong 1970).

Fecundity

We determined the fecundity of female coho salmon from Sashin Creek in 1966, 1970, and 1971 and, for comparison, from nearby Nakvassin Creek in 1966-72 (Table 8). Most of the females from Sashin Creek were collected at the weir and the rest were collected with sport fishing gear in the estuary (a total of 3 to 22 each year). All samples from Nakvassin Creek were collected with sport fishing gear in the estuary (6 to 45 females each year). Ovaries from individual females were placed in containers of water and boiled until the eggs hardened and separated from the ovarian tissues. The mean of the annual fecundity samples from Sashin Creek was 3,186 eggs per female (33 fish); the fish from Nakvassin Creek were slightly smaller and the mean of the samples was 2,326 eggs (116 fish).

The relation between number of eggs and fork length for Sashin Creek and Nakvassin Creek coho salmon was calculated by the method of least squares regression. The regressions for Sashin Creek and Nakvassin Creek are $\hat{Y} = -441.48 + 51.633X$ ($r = 0.31$) and $\hat{Y} = -824.59 + 47.686X$ ($r = 0.37$), respectively. $\hat{Y}$ is the estimated number of eggs and X is the fork length in centimeters of females. Log transformations of number of eggs and fork length did not increase the values of r significantly.

Average fecundities of coho salmon reported for other streams range between 1,983 and 5,343 (Table 9). Although these values were derived in many different ways and therefore are not strictly comparable, a general trend of increasing fecundity from south to north and east to west does appear.

TABLE 8.–Mean and range of fecundity and length of female coho salmon from Sashin Creek in 1966, 1970, and 1971 (3 to 22 fish) and Nakvassin Creek in 1966-72 (6 to 45 fish).

Creek and year	No. of females sampled	Number of eggs		Fork length (cm)	
		Mean	Range	Mean	Range
Sashin Creek:					
1966	8	2,868	1,195-4,418	70.5	64.8-73.7
1970	3	3,472	3,277-3,581	65.6	64.3-68.2
1971	22	3,217	2,537-4,665	69.6	63.1-79.8
Nakvassin Creek:					
1966	7	2,463	1,853-2,931	67.8	64.8-70.0
1967	8	2,143	1,737-2,565	65.6	61.3-70.8
1968	6	2,545	2,086-3,301	66.3	60.0-68.6
1969	15	2,228	1,664-3,120	66.4	56.0-69.5
1970	22	2,294	1,259-3,127	64.1	57.0-67.5
1971	13	2,414	2,000-2,816	66.7	63.5-69.9
1972	45	2,194	1,182-3,574	63.9	56.0-71.0

Retained Eggs

In 1965 and 1967, dying and dead spent female coho salmon were examined for retained eggs

TABLE 9.—Summary of available data on fecundity of coho salmon throughout most of the geographic range.[1] The data are not strictly comparable among the various published and unpublished sources because of differences in methodology. Localities arranged in counterclockwise order from California to Sakhalin Island, USSR.

Area	Average no. of eggs	No. of fish in sample	Average fork length (cm)	Source of data
California:				
Scott Creek	[2]2,616	65	[3]66.3	Shapovalov and Taft (1954)
Oregon:				
Fall Creek, Alsea River	1,983	92	[2]66.2	Koski (1966)
Big Creek	3,030	74	70.2	James R. Graybill (pers. commun. 31 May, 1973)
Washington:				
Minter Creek	2,500	1,120	—	Salo and Bayliff (1958)
University of Washington, Seattle	3,100	63	63	Allen (1958)
British Columbia:				
Cowichan River, Vancouver Island	2,329	—	—	Neave (1948)
Oliver Creek (tributary to Cowichan River)	2,267	—	—	Foerster (1944)
Beadnell Creek (tributary to Cowichan River)	2,789	—	—	Foerster (1944)
Sweltzer Creek	2,300	—	—	Foerster and Ricker (1953)
Fraser River	3,152	48	[4]65.3	Foerster and Pritchard (1936)
Nile Creek	2,310	([5])	—	Wickett (1951)
Namu Cannery	3,002	21	[4]69.8	Foerster and Pritchard (1936)
Port John Creek	2,313	3	—	Hunter (1948)
Alaska:				
Sashin Creek, southeastern	3,186	33	68.6	Present study
Nakvassin Creek, southeastern	2,326	116	65.8	Present study
Bear Creek, Cook Inlet	4,115	193	—	Lawler (1963, 1964)
Bear Creek, Cook Inlet	[6]3,595	179	66.9	Logan (1968)
Dairy Creek, Cook Inlet	4,177	155	72.8	Lawler (1963), Engel (1965) combined
Cottonwood Creek, Cook Inlet	2,346	220	55.1	Andrews (1961), McGinnis (1966) combined
Fish Creek, Cook Inlet	2,426	112	—	Calculated from Andrews (1962)
Swanson River, Cook Inlet	3,448	1,019	62.3	Calculated from Engel (1967)
Lake Rose Tead, Kodiak Island	4,201	—	—	Marriott (1968), Van Hulle (1970) combined
Lake Miam, Kodiak Island	4,209	277	—	Van Hulle (1971)
Karluk River, Kodiak Island	4,706	49	[7]62.1	Drucker (1972)
Union of Soviet Socialist Republics:				
Kamchatka River, Kamchatka	4,683	—	[8]60.4	Kuznetsov (1928)
Bolyshaya River, Kamchatka	4,300-5,343	—	[8]56.5	Semko (1954)
Paratunka River, Kamchatka	4,350	—	[8]59.1	Gribanov (1948)
Tymi River, Sakhalin Island	4,570	—	—	Smirnov (1960)

[1]Table adapted from Rounsefell (1957) and Allen (1958).
[2]Value calculated from regression curve.
[3]Mean length determined from 338 females.
[4]Total length.
[5]Three to eight specimens per year.
[6]After introduction of Swanson River coho salmon stocks into Bear Lake.
[7]Mideye to fork length.
[8]Lengths given by Gribanov (1948), not from females sampled for fecundity.

during daily stream surveys. Only seven spent females were examined each year because high water washed most dying spawners from the stream. The number of eggs ranged from 0 to 64 and averaged 8 per female for the two seasons. Koski (1966) examined 30 spent female coho salmon in an Oregon stream and found an average of four eggs per female. In streams of Kamchatka, Semko (1954) found that coho salmon retained 0.3% of the actual fecundity (about 7 to 16 eggs per female).

JUVENILE COHO SALMON STUDIES

With anadromous salmon, the result of freshwater production is a juvenile migrating to the ocean—a smolt or fry physiologically adapted to enter salt water, where most growth takes place. Our studies were designed to measure the yield of coho salmon smolts and to determine some of the factors that bear on this yield. We counted and sampled the juvenile coho salmon at a weir as they left Sashin Creek and entered the estuary, and also sampled juveniles in the stream with seines. In addition, after determining that many fry of unknown physiological capabilities entered salt water, we performed experiments to determine the ability of these fry to survive the salinities existing in the estuary. For studies in the stream coho salmon juveniles were considered as two groups—fry (age 0) and fingerlings (age I and older).

Specific topics considered here are: 1) the numbers of coho salmon smolts and fry entering

the estuary from Sashin Creek each year, 1956-68; 2) the migration of fry to the estuary and their ability to survive in salt water; 3) age and growth of juveniles in the stream; 4) survival through various life stages (potential egg deposition to fry emergence and as juveniles in the stream); and 5) mortality in fresh water.

Juveniles Entering the Estuary

In Sashin Creek the emergence of coho salmon fry from the gravel usually begins in April and is completed by the end of May, although in especially cold years emergence may not start until June or July. Juvenile coho salmon usually live in Sashin Creek for 1 to 3 yr before migrating to salt water as smolts, but some migrate to the estuary during their first spring or summer as fry. The migration of fry to salt water soon after they emerge has been reported in several other streams (Chamberlain 1907; Gilbert 1913; Pritchard 1940; Wickett 1951; Foerster 1955), but none of these authors reported a substantial return of adult salmon from such early-migrating fry. All of the scale samples from adult coho salmon at Sashin Creek indicated that the fish had spent at least 1 yr in fresh water. The absence of adults originating from early-migrating fry suggests very poor survival of fry entering the estuary at a small size (usually <35 mm from Sashin Creek), which could be the result of heavy predation or some failure to adapt physiologically to the marine environment. We have assumed that we can identify adults derived from early-migrating fry on the basis of the pattern of circuli on their scales. However, if fry surviving in the estuary developed scale patterns indistinguishable from those of fry spending a year or more in fresh water, our assumption that age 0 emigrants did not contribute to the adult run could be incorrect.

Numbers of Fry and Smolts

Counts and estimates of the numbers of juvenile coho salmon migrating from Sashin Creek ranged from 218 to 44,023 fry and 928 to 2,865 smolts between 1956 and 1968 (Table 10). In 1964, 44,023 fry left the stream between 19 April and 28 August, and most migrated in a 2-wk period in mid-June—the greatest migration was 3,528 fry on 15 June. The smolt migration in Sashin Creek varied about threefold from 1956 through 1968 (excluding 1965-66—Table 10). The relatively low counts of smolts in 1964 probably resulted from a change in the trapping procedures at the weir. Before 1964, all fish migrating from Sashin Creek were captured. The procedures used in 1964 were designed to capture a portion of the emigrating fry and did not retain smolts well. Because of high water and ice damage to the weir, complete counts of emigrating fry and smolts were not made for 1965-67. In 1965 and 1967, estimates of fry and smolts were based on catches in fyke nets that sampled the migrants at the weir site. No estimates were obtained in 1966.

A comparison of the time of smolt migration from Sashin Creek with the time of migration from streams and lakes along the eastern Pacific coast from south-central Alaska to central coastal California indicates that there is a tendency

TABLE 10.—Numbers and times of migration of coho salmon fry and smolts past the Sashin Creek weir and yield of smolts, 1956-68.[1]

Year	Number counted at weir[2]		Counting period	Date of largest migration		Date last fish was observed to emigrate		Yield of smolts per 100 m² of rearing area
	Fry	Smolts		Fry	Smolts	Fry	Smolts	
1956	—	928	16 Apr.-30 June	—	15 June	—	20 June	5.5
1957	373	1,961	10 Apr.-29 June	17 June	24 May	27 June	27 June	11.5
1958	2,854	1,015	7 Mar.-3 June	4 May	20 May	31 May	2 June	6.0
1959	218	1,587	1 Apr.-21 July	14 July	27 May	15 July	3 July	9.3
1960	9,923	1,258	17 Mar.-2 July	12 June	10 June	30 June	30 June	7.4
1961	2,699	2,489	22 Mar.-19 June	21 May	28 May	17 June	17 June	14.6
1962	1,209	2,865	11 Mar.-4 July	14 June	27 May	4 July	3 July	16.9
1963	1,236	1,599	11 Mar.-8 July	30 May	24 May	1 July	3 July	9.4
1964	44,023	[3]334	15 Mar.-28 Aug.	15 June	24 May	28 Aug.	6 July	—
1965[4]	12,000	—	11 Apr.-30 July	24 June	—	15 July	—	—
1967[4]	10,000	1,400	10 Apr.-8 Aug.	28 June	25 May	8 Aug.	5 July	8.2
1968	1,665	1,440	26 Mar.-3 Aug.	5 June	24 May	3 Aug.	5 July	8.5

[1]The year 1966 is not included because the weir was damaged and substitute sampling was not conducted.
[2]Daily counts for 1956-64, available from Olson and McNeil (1967).
[3]Counting procedure changed from total to partial counts; holding facilities were inadequate for retaining all smolts captured.
[4]Weir not functional; fyke net(s) fished to sample a portion of the spring emigration. Numbers of fry and smolts presented are estimates made from fyke net catches.

toward earlier migration in the southern part of the range (Table 11).

To compare yields of coho salmon smolts between streams, we express yield in numbers per unit area. Estimates of the annual yield of coho salmon smolts from Sashin Creek for the period 1956-68 (except 1964-66) ranged from 5.5 to 16.9/100m^2 of rearing area (Table 10). The yield of smolts for a 5-yr period in three streams tributary to Drift Creek ranged from 18 to 67/100 m^2 (Chapman 1965). The much lower yield of smolts from Sashin Creek probably reflects increased mortality accompanying the additional 12 mo of freshwater residence for most smolts from Sashin Creek. The number of nonmigrant yearling coho salmon in Sashin Creek in early summer (determined from population studies) approximates the yield of smolts from Drift Creek tributaries more closely than does the yield of smolts (all ages) from Sashin Creek.

Early Emigration and Salinity Tolerance of Fry

The number of fry entering the estuary is great enough (Table 10) that the question of their fate in salt water is important. Many factors such as predation, failure to find adequate food, failure to adjust physiologically to salt water, and disease may act alone or in combination to determine the survival of fry entering marine waters. We had opportunity to explore adjustment to salt water as a factor in survival of migrating fry.

Early-migrating coho salmon fry might have reentered Sashin Creek undetected, although they could not have done so while the fry and smolt weir was in operation. In addition, a low waterfall immediately downstream from the weir is a barrier to upstream migration of coho salmon fry except for several days each year when above-average high tides inundate the falls. Our popula-

TABLE 11.—Timing of seaward migration of coho salmon smolts from streams and lakes in Alaska, British Columbia, Washington, Oregon, and California.

Location	Migration period	Peak of migration	Source of data
South-central Alaska:			
Fire Lake (lat. 61°21′N)	Mid May-early July	Late May-early June	Wallis (1967, 1968)
Bear Lake (lat. 60°12′N)	Late May-early Aug.	Early June	Logan (1963)
Little Kitoi Lake, Afognak Island (lat. 58°12′N)	Late May-late July	Mid June	Parker and Vincent (1956)
Karluk Lake, Kodiak Island (lat. 57°27′N)	Mid May-early July	Late May-early June	Drucker (1972)
Lake Margaret (lat. 57°46′N)	Mid Mar.-early July	Late May-early June	Van Hulle (1971)
Lake Genivieve (lat. 57°46′N)	Mid May[1]-mid July	Late May-early June	Van Hulle (1971)
Souhteastern Alaska:			
Taku River (lat. 58°33′N)	Mid Apr.-mid June[2]	Mid May-early June	Meehan and Siniff (1962)
Eva Lake (lat. 57°24′N)	Mid May-mid June	Late May	Armstrong (1970)
Hood Bay Creek (lat. 57°20′N)	Early May-late June	Mid May-early June	Armstrong (1970)
Sashin Creek (lat. 56°23′N)	Apr.-early July	Late May-early June	Table 10, this report
Central coastal British Columbia:			
Port John (Hooknose Creek) (lat. 52°08′N)	Mid Apr.-early June	May	Hunter (1948, 1949)
Southern British Columbia:			
Cultus Lake (lat. 49°03′N)	Apr.-June	Late May-early June	Foerster and Ricker (1953)
West-central Washington:			
Minter Creek (lat. 47°22′N)	Feb.-early June	May	Salo and Bayliff (1958)
Northwestern Oregon:			
Gnat Creek (lat. 46°12′N)	Apr.-early June	May	Willis[3]
Northern coastal Oregon:			
Spring Creek (lat. 45°36′N)	Late Feb.-May	Late Mar.-early May	Willis et al.[4]
Central coastal Oregon:			
Drift Creek tributaries: Deer, Flynn, and Needle Branch Creeks (lat. 44°32′N)	Feb.-May	Late Mar.-early Apr.	Chapman (1962, 1965)
Crooked Creek (lat. 44°25′N)	Feb.-early June	Apr.-May	Harry H. Wagner (pers. commun. 9 July 1973)
Southern coastal Oregon:			
Sixes River (lat. 42°51′N)	Mar.-June	Apr.-May	Reimers[5]
Central coastal California:			
Waddell Creek (lat. 37°06′N)	Apr.-early June	Late Apr.-May	Shapovalov and Taft (1954)

[1]Trapping facilities were completed after the beginning of the migration.
[2]Period when a sampling trap was operated.
[3]Willis, R. A. 1962. Gnat Creek weir studies. Final Rep., BCF Contract 14-17-0001-469, Fish Comm. Oreg., Res. Div., 71 p.
[4]Willis, R. A., R. N. Breuser, A. L. Oakley, and R. W. Hasselman. 1959. Coastal Rivers Investigations Prog. Rep., August 1957-June 1958, Fish Comm. Oreg., 24 p.
[5]Reimers, P. E. 1971. The movement of yearling coho salmon through Sixes River estuary. Coastal Rivers Investigations Prog. Rep. 71-2, Fish Comm. Oreg., 15 p.

tion studies of juvenile coho salmon in Sashin Creek suggest that no large-scale reentry of coho salmon fry occurs.

Coho salmon fry from an Oregon coast stream adjusted to water of moderately high salinities in laboratory tests (Conte et al. 1966). Our field observations, live-box experiments, and bioassays at Little Port Walter confirm that ability for fry from Sashin Creek. In July 1964, after about 44,000 coho salmon fry had migrated from Sashin Creek, schools of fry were seen near the surface of the inner bay. Most of them appeared to be in water of low salinity above a density interface about 30 cm deep, but they retreated to deeper more saline waters when disturbed.

To study the ability of coho salmon fry to adjust to the saline conditions in the Little Port Walter estuary, some fry were confined in live-boxes in the inner bay during the summer of 1964. Two sizes of live-boxes were used: six small boxes (86 by 86 by 122 cm deep) were arranged so that the water depth in the box was 81 cm, and two large boxes (122 by 122 by 244 cm deep) were suspended from a floating frame so that water depth was 235 cm. The small boxes were arranged in three sets of two boxes each, and 60 fry were placed in each box; the fry were from the weir trap, the inner bay, and Sashin Creek. Twenty-five fry from the inner bay were placed in each of the large boxes.

Initially, the Sashin Creek and weir trap fry in the live-boxes entered high-salinity water for short periods only, whereas some inner bay fry remained in the high-salinity water for long periods. Most of the fry stayed at or near the density interface close to the top of the box where the salinity was 14‰ or less; but some, especially those from the inner bay, swam for extended periods near the bottom of the box where salinity was 28 to 29‰.

Survival and growth of the fry seemed to be related more to the size of the live-box and the resulting competition for food than to the fry's ability to adjust to the saline water of the bay. In the small live-boxes, during the first 5 days 3% of the fry died and in 30 days 26% had died; in the large live-boxes in 35 days only 8% of the fry died (Table 12). The general comparison is true both for the entire small-box group versus the large-box group and for the small-box group of fish from the inner bay versus the large-box group (also from the inner bay). No supplemental food was provided, and the fry in the small boxes grew very little or not at all, whereas those in the large boxes grew about 5 mm (Table 12).

Tests were conducted in July 1964 to measure the ability of coho salmon fry to survive abrupt transfer to higher salinity waters. Salinities were determined with hydrometers. Plastic buckets were used as test containers, and as in the live-box studies, coho salmon fry were taken from Sashin Creek, the weir trap, and the inner bay. For each test, 10 fish were abruptly transferred from their source water to the test water. The fry from all three sources survived 48 h in salinities up to 23.5‰ (Table 13). In 29‰ water, the fry from the inner bay lived for 48 h, but none of those from the weir trap and only 50% of those from Sashin Creek survived 48 h. Of seven fry from the weir trap that survived 96 h in 17.6‰ salinity, three were transferred to 31‰ for 48 h, and one survived; four were transferred to 23.5‰ and three survived for 48 h. Seven fry that survived 96 h in 23.5‰ salinity were transferred to 31‰—four of these fry were still alive 48 h later when the experiment was

TABLE 12.—Mortality and growth of coho salmon fry held in live-boxes in the inner bay of Little Port Walter in the summer of 1964.

Size of live-box and no. of fish	Source of fish	Total mortality after			Average initial fork length of fry (mm)	Average fork length at end of experiment (mm)
		5 days	30 days	35 days		
Small:						
60	Weir trap	2	13	[1]	36.8	35.9
60	Inner bay	2	15	[1]	38.6	38.6
60	Weir trap	6	24	[1]	36.8	35.7
60	Sashin Creek	1	18	[1]	36.8	36.8
60	Inner bay	0	13	[1]	38.6	38.9
60	Sashin Creek	0	11	[1]	36.8	36.4
Large:						
25	Inner bay	[2]	[2]	1	40.0	44.7
25	Inner bay	[2]	[2]	3	40.0	45.4

[1]Experiment terminated after 30 days.
[2]No observations until day 35.

TABLE 13.—Cumulative deaths of coho salmon fry taken from the inner bay of Little Port Walter, the weir trap at the mouth of Sashin Creek, and Sashin Creek and held in waters of various salinities, July 1964.

Salinity (‰)	Number of fish	Source of fish	Size range (fork length, mm)	Cumulative deaths at				
				24 h	48 h	72 h	96 h	144 h
0	10	Weir trap	32-38	0	0	0	0	0
0	10	Inner Bay	37-45	0	0	[1]	—	—
0	10	Weir trap	35-39	0	0	[1]	—	—
0	10	Sashin Creek	35-41	0	0	0	—	—
2.2	10	Inner Bay	36-47	0	0	[1]	—	—
12.5	10	Inner Bay	35-40	0	0	[1]	—	—
12.5	10	Weir trap	35-42	0	0	0	—	—
12.5	10	Sashin Creek	38-45	0	0	0	—	—
17.6	10	Weir trap	33-39	0	0	1	3	[2][6]
19.3	10	Weir trap	34-39	0	0	0	—	—
19.3	10	Sashin Creek	34-63	0	0	0	—	—
23.5	10	Weir trap	33-40	0	0	0	0	0
23.5	10	Weir trap	32-40	0	0	3	3	[3]6
29	10	Inner Bay	31-42	0	0	2	—	—
29	10	Weir trap	29-35	8	10	—	—	—
29	10	Sashin Creek	33-52	1	5	[1]	—	—
31	20	Weir trap	31-42	18	20	—	—	—

[1]Accidentally discontinued before 72 h.
[2]Of seven survivors in 17.6‰ at 96 h, three were transferred to 31‰ for 48 h, and one survived; four were transferred to 23.5‰, and three survived for 48 h.
[3]Period from 96 to 144 h at 31‰ salinity.

ended (Table 13). Otto (1971) found that salinity tolerance of juvenile coho salmon was increased by a 35-day exposure to water of lower salinity.

The inner bay has horizontal and vertical salinity gradients (Powers 1963), which are excellent for acclimation of young salmon to salt water. Much of the surface of the inner bay is usually less than 10-15‰ salinity. Our bioassays show that fry able to survive 48 h in 23‰ salinity should be able to acclimate fully to salinities encountered in the inner bay if they have access to the low salinity refuge. Our observation of coho salmon fry in live-boxes confirms this ability.

Juveniles in the Stream

Age Determination

Because length frequencies of different age-groups can overlap broadly at some times of the year (Figures 5-7), scales of juvenile coho salmon were analyzed to assign age-groups. Analysis of scale samples indicated that an average of 11% of all fingerlings (age I and older) collected from the stream were age II. Sizes of the various age-groups sampled by month for 1964-67 are shown in Figure 5.

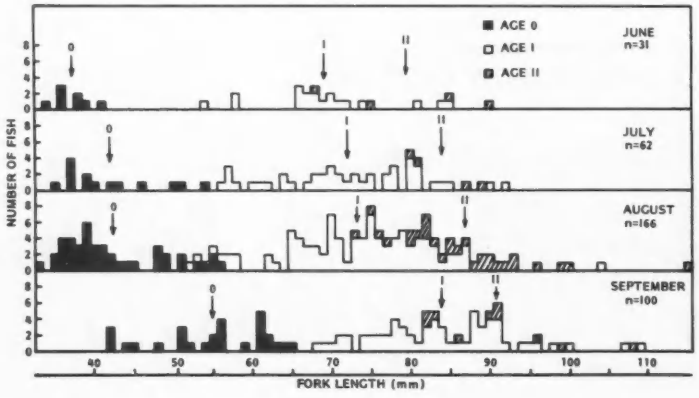

FIGURE 5.—Length frequencies and ages of coho salmon juveniles from Sashin Creek grouped by month of collection, June to September 1964-67. Ages were determined by analysis of scale samples, and lengths were measured on preserved fish. Arrows indicate location of mean lengths for each age class.

Most coho salmon fry (age 0) collected in June were under 40 mm in fork length and had not formed scales. Gribanov (1948) found that the scale covering usually appeared on young coho salmon from Kamchatka at 40 mm long.

Growth and Age Characteristics

Growth of juvenile coho salmon in Sashin Creek was determined from fork lengths (measured to the nearest millimeter) of samples of fry and fingerlings. Fry were collected periodically during summer 1964, and fry and fingerlings were captured during each of several population estimates of juveniles in Sashin Creek during 1965-67. An additional 50 fry from each of the three study areas of Sashin Creek were measured in mid-July 1966 and mid-August 1967. Samples of fingerlings from the three study areas were measured in early July, early August, and mid-September 1968.

There was no consistent difference in the mean fork lengths of corresponding age groups of juvenile coho salmon captured in the upper, middle, or lower areas in any sampling period (Table 14). Juveniles from Funny Creek were usually slightly smaller than those from Sashin Creek during a corresponding period.

The length data for juvenile coho salmon sampled in Sashin Creek for 1964-68 have been combined by month for fry and fingerlings (Figure 6). The difference between the fork length of fry and fingerlings was pronounced in early summer, but by July the lengths of fast-growing fry and slow-growing fingerlings overlapped (Figure 6). Occasionally it was difficult to assign the proper age-group to juveniles in the overlapping sizes, although they could usually be separated by the brightly colored and proportionally longer fins and smaller eyes of the fry.

The average fork length of coho salmon fry in Sashin Creek in October is about 60 mm. The average length of those that do not become smolts the following spring but remain in the stream a second year is usually 65-75 mm by July. In the 1968 migration, age I smolts averaged 83 mm, age II smolts 105 mm, and age III smolts 104 mm (Figure 7). In comparison, in 1968 coho salmon from Hood Bay Creek in southeastern Alaska averaged 83 mm fork length as age I smolts and 96 mm as age II smolts; in 1969 age I smolts averaged 79 mm and age II smolts 91 mm (Armstrong 1970). For the years 1956, 1965, and 1968, coho salmon smolts migrating from Karluk Lake, Kodiak Island, Alaska, averaged 111 mm as age I smolts, 139

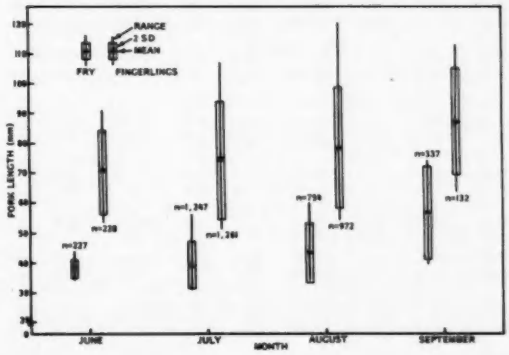

FIGURE 6.—Mean and range of fork lengths of fry (age 0) and fingerling (ages I and II) coho salmon, Sashin Creek, 1964-68. Lengths were measured from live fish.

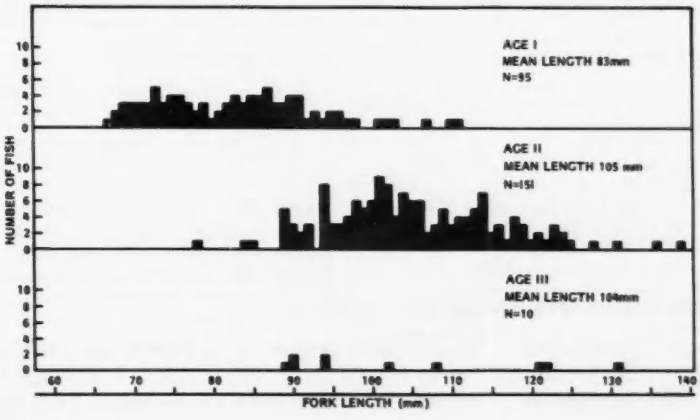

FIGURE 7.—Length frequencies of ages I, II, and III coho salmon smolts, Sashin Creek, 1968. Total sample was 256 fish, of which 37% were age I, 56% age II, and 4% age III. Ages were determined by analysis of scale samples, and lengths were measured on live fish.

TABLE 14.—Fork length (mm) of coho salmon fry and fingerlings captured in three study areas of Sashin Creek and Funny Creek, 1964-68.

Date[1] and type of sample	Sashin Creek												Funny Creek		
	Upper area			Middle area			Lower area			Total					
	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.
1964:															
7 July:															
Fry	—	—	—	—	—	—	—	—	—	31-46	36.8	43	—	—	—
15 July:															
Fry	—	—	—	—	—	—	—	—	—	33-49	39.8	92	—	—	—
21 July:															
Fry	—	—	—	—	—	—	—	—	—	32-46	37.0	34	—	—	—
28 July:															
Fry	—	—	—	—	—	—	—	—	—	34-50	39.2	91	—	—	—
31 July:															
Fry	—	—	—	—	—	—	—	—	—	33-52	38.9	39	—	—	—
18 Aug.															
Fry	—	—	—	—	—	—	—	—	—	37-59	45.1	56	—	—	—
1965:															
17 July:															
Fry	34-44	38.5	37	34-44	38.0	43	35-45	38.1	103	34-45	38.2	183	—	—	—
Fingerlings	55-80	67.7	71	53-90	68.8	99	51-86	69.7	147	51-90	69.0	317	—	—	—
1 Aug.:															
Fry	—	—	—	—	—	—	—	—	—	—	—	—	37-43	39.1	29
Fingerlings	—	—	—	—	—	—	—	—	—	—	—	—	47-80	62.1	28
11 Aug.:															
Fry	39-47	41.9	17	37-46	40.5	12	35-49	40.3	99	35-49	40.5	128	35-46	39.1	84
Fingerlings	56-84	73.4	24	56-90	70.6	96	54-91	70.2	102	54-91	70.7	222	49-91	63.8	43
30 Sept.:															
Fry	45-74	62.2	73	59-69	64.3	7	49-69	60.4	7	45-74	62.2	87	39-70	53.4	61
Fingerlings	76-104	88.0	11	84	84	1	75-97	86.0	2	75-104	87.4	14	71-105	85.8	44
1966:															
27 June:															
Fry	35-40	37.0	34	34-43	37.4	133	35-44	39.3	60	34-44	37.9	227	34-39	36.6	61
Fingerlings	60-89	71.9	24	53-85	67.6	69	56-91	71.8	135	53-91	70.6	228	50-98	72.1	78
8 July:															
Fry	35-43	37.7	24	33-47	37.7	95	34-50	40.3	101	33-50	39.0	220	34-50	38.0	102
Fingerlings	62-93	77.9	48	58-95	75.4	45	56-104	77.5	56	56-104	77.0	149	50-102	70.6	105
14 July:															
Fry	34-44	37.8	50	33-46	38.9	50	36-47	39.5	50	33-47	38.7	150	36-47	39.9	50
29 July:															
Fry	34-56	46.4	50	36-53	42.4	53	36-55	43.0	51	34-56	43.9	154	33-56	40.8	54
Fingerlings	55-98	76.3	63	65-105	79.1	58	68-102	81.6	45	55-105	78.7	166	61-105	75.5	50
14 Aug.:															
Fry	38-58	48.1	100	36-59	46.2	100	37-60	46.2	100	36-60	46.8	300	32-63	44.7	100
Fingerlings	60-102	82.0	89	63-107	84.2	100	65-106	84.6	100	60-107	83.7	289	56-119	81.1	100
8 Sept.:															
Fry	44-68	57.3	50	39-67	49.6	100	46-68	58.0	100	39-68	54.5	250	40-68	52.1	100
Fingerlings	67-102	86.7	50	63-95	81.5	10	69-113	87.8	36	63-113	86.6	96	61-108	85.3	100
1967:															
23 July:															
Fry	33-41	36.5	50	34-45	37.9	71	33-52	38.8	120	33-52	38.0	241	36-42	37.9	50
Fingerlings	52-104	70.8	100	53-93	69.5	105	53-92	72.8	112	52-104	71.1	317	52-103	77.1	107
4 Aug.:															
Fry	—	—	—	—	—	—	34-49	38.6	116	34-49	38.6	116	35-50	40.2	75
Fingerlings	—	—	—	—	—	—	57-104	76.2	228	57-104	76.2	228	55-104	74.3	50
17 Aug.:															
Fry	36-46	40.7	50	35-50	40.9	54	37-55	41.1	50	35-55	40.9	154	—	—	—
5 Sept.:															
Fry	—	—	—	—	—	—	—	—	—	—	—	—	38-64	46.3	38
Fingerlings	—	—	—	—	—	—	—	—	—	—	—	—	72-90	81.0	3
17 Oct.:															
Fry	—	—	—	—	—	—	—	—	—	—	—	—	45-69	59.5	159
Fingerlings	—	—	—	—	—	—	—	—	—	—	—	—	70-97	79.8	27
1968:															
2 July:															
Fingerlings	56-96	74.6	110	59-103	80.0	98	59-107	83.2	104	56-107	79.2	312	57-103	77.9	74
1 Aug.:															
Fingerlings	59-101	76.9	68	57-104	82.2	80	66-120	81.3	85	57-120	80.3	233	59-107	82.4	62
20 Sept.:															
Fingerlings	79-100	88.7	22	—	—	—	—	—	—	79-100	88.7	22	—	—	—

[1]Dates given for 1965, 1966, 1967, and 1968 measurements are middates of the measuring period.

mm as age II smolts, 151 mm as age III smolts, and 175 mm as age IV smolts (Drucker 1972). Kamchatka streams at about the same latitude as Sashin Creek produce 40- to 70-mm coho salmon fry by September (Gribanov 1948), 85-mm age I smolts, and 130-mm age II smolts (Semko 1954). In

California (Shapovalov and Taft 1954) and British Columbia (Foerster and Ricker 1953), the mean lengths of coho salmon smolts (mostly age I) usually ranged from 110 to 120 mm.

In coho salmon, attaining the smolt stage is apparently more a function of size than age. Data on lengths and numbers of juvenile coho salmon in Sashin Creek during September and early summer suggest that most require two summers of freshwater residence to reach smolt size. Coho salmon can grow much faster; some juveniles in a brackish pond in Oregon grew from about 40 mm (890 to the pound) to about 120 mm and became smolts in only 3 mo instead of the usual 1 yr (Garrison 1965).

The growth of juvenile coho salmon in Sashin Creek varies from year to year. During summer 1966, for instance, fry were larger than in 1964, 1965, and 1967 (Figure 8). In the summers of 1966 and 1968, fingerlings (mainly age I) were larger than in 1965 and 1967 (mainly age I). The number of fingerlings in 1966 and 1968[4] (≈3,000 on 1 July) was less than in either 1965 (≈5,000 on 1 July) or 1967 (≈3,500 on 1 July), and less competition for food would be expected and could account for the larger size of the fingerlings in 1966. Also, the presence of fewer fingerlings in summer 1966 may have allowed the fry to reach a larger size because of less competition for food or space. Food abundance, controlled by factors other than coho salmon population size, may have an important influence on coho salmon growth in Sashin Creek. We have no information on possible year-to-year differences in food supply independent of fish populations which could result in differences in growth of juvenile coho salmon.

[4]An estimate of 2,960 fingerlings in Sashin Creek was made on 2 July 1968.

Survival from Potential Egg Deposition to Emergence

The estimated potential egg depositions for brood years 1963, 1964, and 1965 were determined by multiplying the mean fecundity (determined from 1966, 1970, and 1971 samples) by the estimated number of females (one-half of the estimated population of spawners). These estimates are considered to be only rough approximations: 1,460,000 for 1963; 260,000 for 1964; and 350,000 for 1965.

Estimates of the numbers of preemerged salmon alevins in the streambed were obtained in the early spring by hydraulic streambed sampling (McNeil 1964). In Sashin Creek this sampling is done to estimate the number of pink salmon alevins, but after relatively large escapements of coho salmon reliable estimates of the number of coho salmon alevins in the streambed also can be made. No coho salmon alevins were found during the hydraulic streambed sampling in the spring of 1966, so the estimate of the alevin population was zero. Because many age 0 fry were in the stream in the summer of 1966, we have estimated the number of alevins that were in the gravel that spring by interpolation of the survivorship curves.

The numbers of preemerged coho salmon alevins for 1964-66 estimated from the results of hydraulic sampling or interpolation of survivorship curves are: 214,000 in spring 1964 (1963 brood year), 58,000 in spring 1965 (1964 brood year), and 100,000 in spring 1966 (1965 brood year). From these figures and estimates of potential egg deposition, we calculated survival from potential egg deposition to just before fry emergence to be 15%, 22%, and 26% for the 1963, 1964, and 1965 brood years, respectively.

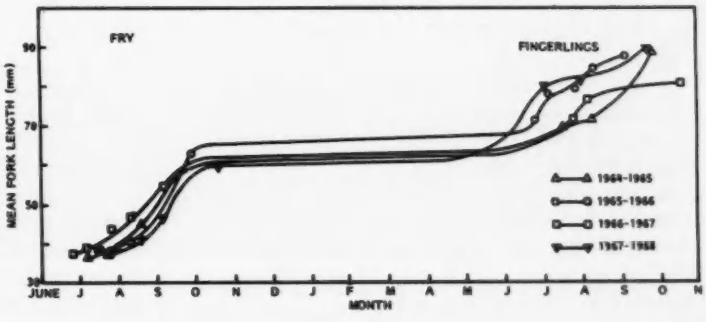

FIGURE 8.—Mean fork lengths of coho salmon fry measured several times each summer, 1964-67, and resulting fingerlings (≈90% age I and 10% age II) the next summer, 1965-68, Sashin Creek.

Survival of Juveniles in Sashin Creek

We estimated the population periodically during the summers from 1964 through 1967 to establish curves depicting changes in the number of juvenile coho salmon by brood year during their freshwater life. In 1964 the numbers of fry were estimated in July and August. In 1965 the numbers of fingerlings (predominantly age I, the balance age II) and fry were estimated in July and August. In 1966 the numbers of fingerlings and fry were estimated in June, July, and September. In 1967 estimates were made of coho salmon fingerlings and fry in Sashin Creek in July and in Funny Creek in July and August.

Juvenile salmon in the stream were captured by a combination of baiting and seining. A homogenized mixture of salmon eggs, ovarian tissue, and water was prepared with an electric blender and injected into the stream at the seining site (Figure 9). Underwater observations indicated that several squirts of the egg solution from a plastic squeeze bottle were adequate to attract rainbow trout, Dolly Varden, coastrange sculpins, and coho salmon fingerlings and large fry from at least 30 m downstream. The downstream sides of gravel bars, logs, and rocks were chosen as collecting sites because these obstructions formed slow-water areas in which the bait would linger for several minutes. In some instances it was necessary to construct a rock barrier to divert the current and create a suitable site. During early summer, when coho salmon fry are quite small, they congregate along the shallow edges of the stream and in backwaters. These small fry will not travel far in response to bait, and we often had to seine for them along the stream edges and backwaters near the baiting site.

Captured fish were anesthetized with MS-222 Sandoz[5] and marked by removing part of one fin. A different fin clip was used for each marking date within a summer. When they recovered from the anesthetic, the marked fish were released at the collection site.

To allow the marked juveniles to become redistributed, we did not begin to recapture them until several days after they were marked. To reduce bias in the population estimate, we selected random points as seining sites during the recapture portion of the experiment. Random numbers between 0 and 99 were chosen from a table of random numbers (Snedecor 1956) for each of the 30.5-m (100-foot) sections of stream. The numbers chosen represented the distance in feet downstream from the origin of each section to the sites that would be baited. These distances were paced off, and one or several places across the width of the stream at the site were baited. A site was repeatedly baited and seined until only a few fish could be taken in each seine haul. All fish captured at a site were anesthetized and examined for marks. When they recovered from the anesthetic, the fish were released. The numbers of unmarked and marked coho salmon juveniles were recorded for each site.

The Bailey-Petersen mark-and-recapture method (Ricker 1958) was used to make all population estimates, except in August 1964 when a Schnable multiple mark-and-recapture method (Ricker 1958) was used for fry. In 1966 and 1967 the numbers of juveniles to be marked and recaptured were predetermined to obtain preassigned levels of accuracy and precision of population estimates (Robson and Regier 1964). We tried to mark and recapture enough fish to be 95% certain that the error in estimating the population was not more than 10% (Table 15). Confidence limits to population estimates were obtained by methods given by Ricker (1958) and Robson and Regier (1968).

The number of coho salmon fry decreased greatly between the first and second estimate (Tables 15, 16). In the month between estimates, the population dropped by 71% in 1964, 78% in 1965, and 62% in 1966. Weir counts of emigrant coho salmon fry, which were continued until mid-August in 1964, showed that only about 2,000 fry (4% of the first population estimate) left Sashin Creek between mid-July and mid-August population estimates. Fyke net catches indicated that even fewer fry migrated from the stream in 1965 and 1966 than in 1964. Therefore, we attribute the large decrease in number of fry each year to mortality rather than emigration. Observation of the activities of fish and avian predators led us to believe that predation probably accounted for the major portion of the mortality. The number of fingerling coho salmon also decreased as the summer progressed, although not as rapidly as the number of fry (Table 17).

The fry population was greater in 1964 than in 1965, 1966, or 1967 as a result of the large number of spawners entering Sashin Creek in the fall of 1963. The population of fingerlings in 1965 was also greater than in 1966 or 1967; the fingerlings in 1965

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

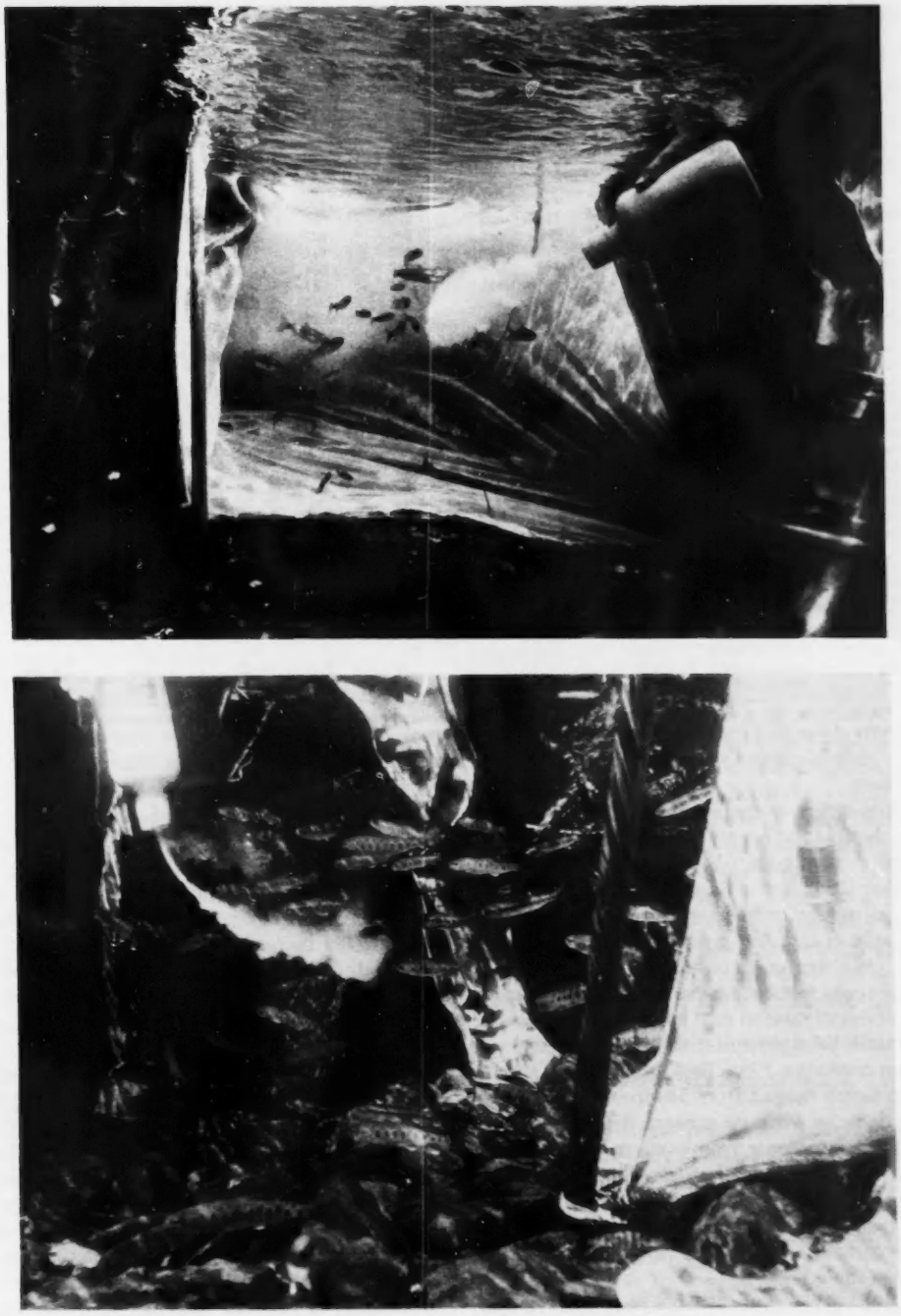

FIGURE 9.—Underwater views of technique used to capture juvenile coho salmon, Sashin Creek. Bait is a blended mixture of salmon eggs, ovarian tissue, and water.

TABLE 15.—Population estimates of juvenile coho salmon from mark-and-recapture experiments in Sashin Creek and Funny Creek, 1964-67.

Middate of estimate	Location	Fin clip used[1]	Age-group	Number marked	Census sample size	Number of marked fish recaptured	Population estimate	95% confidence interval
1964:								
12 July	Sashin Creek	LV&RV	Fry	1,454	4,421	123	51,852	43,939-62,216
12 Aug.	Sashin Creek	ULC	Fry	1,475	1,929	174	15,185	12,530-17,840
1965:								
17 July	Sashin Creek	RV	Fry	1,601	485	42	20,355	14,849-28,039
17 July	Sashin Creek	RV	Fingerlings	510	520	57	4,581	3,659- 5,960
1 Aug.	Funny Creek	LLC	Fry	276	221	50	1,201	900- 1,601
1 Aug.	Funny Creek	LLC	Fingerlings	213	107	26	852	565- 1,283
11 Aug.	Sashin Creek	LV	Fry	847	804	149	4,546	3,965- 5,294
11 Aug.	Sashin Creek	LV	Fingerlings	949	581	143	3,836	3,356- 4,459
11 Aug.	Funny Creek	LV	Fry	221	244	54	984	762- 1,300
11 Aug.	Funny Creek	LV	Fingerlings	106	141	26	557	370- 841
1966:								
27 June	Sashin Creek	ULC	Fry	2,263	2,541	163	35,077	30,436-40,951
27 June	Sashin Creek	ULC	Fingerlings	332	520	59	2,883	2,312- 3,731
27 June	Funny Creek	ULC	Fry	716	509	225	1,616	1,474- 1,793
27 June	Funny Creek	ULC	Fingerlings	78	160	49	251	187- 328
29 July	Sashin Creek	LLC	Fry	3,002	2,957	660	13,434	12,584-14,394
29 July	Sashin Creek	LLC	Fingerlings	816	817	420	1,585	1,488- 1,701
29 July	Funny Creek	LLC	Fry	208	338	67	1,037	816- 1,300
29 July	Funny Creek	LLC	Fingerlings	223	257	147	389	354- 442
8 Sept.	Area U[2]	Anal	Fry	227	378	93	915	757- 1,081
8 Sept.	Area U[2]	Anal	Fingerlings	63	155	20	468	293- 755
8 Sept.	Funny Creek	Anal	Fry	287	314	146	615	552- 700
8 Sept.	Funny Creek	Anal	Fingerlings	110	100	34	317	221- 451
1967:								
23 July	Sashin Creek	ULC	Fry	1,604	1,015	131	12,346	10,616-14,604
23 July	Sashin Creek	RV	Fingerlings	1,431	890	418	3,043	2,848- 3,274
23 July	Funny Creek	ULC	Fry	202	213	53	801	622- 1,092
23 July	Funny Creek	RV	Fingerlings	289	359	206	503	459- 551
17 Aug.	Sashin Creek	Anal	Fry	996	—	—	—	—
17 Aug.	Sashin Creek	Anal	Fingerlings	807	—	—	—	—
17 Aug.	Funny Creek	Anal	Fry	249	158	18	2,084	1,383- 3,381
17 Aug.	Funny Creek	Anal	Fingerlings	354	27	7	1,239	745- 3,218

[1]LV, RV, ULC, LLC, and Anal refer to left pelvic, right pelvic, upper lobe of caudal, lower lobe of caudal, and anal fin clips, respectively.
[2]Estimates of population size in the whole of Sashin Creek were not made.

were mainly progeny of the abundant 1963 spawners.

Variations in average annual streamflow have been shown to affect significantly the number of juvenile coho salmon in Washington streams (Smoker 1953), but in Sashin Creek, other factors such as parent escapement, original number of coho salmon fry, and competition probably have more influence on determining the number of juvenile coho salmon. Sashin Creek is located in an area of heavy rainfall that has small variations in the annual total precipitation and annual average stream discharge. From 1964 through 1967, annual precipitation ranged from 546 to 643 cm. Greater variations in average stream discharge for a specific month occur from year to year. Annual variations in stream discharge during the 1-mo period in midsummer when populations of juvenile coho salmon decreased most rapidly do not appear to be correlated with the rates of population decline (Table 17).

In 1965, 1966, and 1967, when estimates of juvenile coho salmon populations were made in each study area, the highest densities of coho salmon in Sashin Creek usually occurred in the lower study area, which is characterized by slow water. Densities of coho salmon fry and fingerlings were even higher in Funny Creek, another slow-water habitat (Table 18).

Funny Creek was unique in our study areas in that the populations of juvenile coho salmon sometimes increased during the summer. The estimated number of coho salmon fingerlings increased from 251 to 389 between late June and late July in 1966 (1964 brood year) and from 503 to 1,239 between mid-July and mid-August in 1967 (1965 brood year); the number of fry increased from 801 to 2,084 between mid-July and mid-August in 1967 (1966 brood year) (Table 16). The 95% confidence interval estimates (Table 15) indicate that the populations did increase, and the additional coho salmon juveniles must have immigrated to this area from Sashin Creek. On all other occasions, in both streams the populations of fry and fingerlings decreased between estimates. The movement of juvenile coho salmon from Sashin Creek into Funny Creek during midsummer suggests the use of this small tributary stream as a

TABLE 16.—Population estimates of juvenile coho salmon of brood years 1963-66[1] in Sashin Creek and Funny Creek in the summers of 1964-67. Separate estimates are included for three areas of Sashin Creek.

Brood year and area	Number of fish (by brood year) on									
	12 July 1964	12 Aug. 1964	17 July 1965	1 Aug. 1965	11 Aug. 1965	27 June 1966	29 July 1966	8 Sept. 1966	23 July 1967	17 Aug. 1967
1963:										
Sashin Creek:										
Upper	—	—	668	—	593					
Middle	—	—	1,216	—	1,115					
Lower	—	—	2,533	—	2,079					
Stream estimate	51,852	15,185	4,581	—	3,836					
Funny Creek	—	—	—	852	557					
1964:										
Sashin Creek:										
Upper			2,979	—	254	402	509	468		
Middle			2,195	—	951	690	555	—		
Lower			14,738	—	3,477	1,562	555	—		
Stream estimate			20,355	—	4,546	2,883	1,585	[2]1,350		
Funny Creek			—	1,201	984	251	389	317		
1965:										
Sashin Creek:										
Upper						1,192	1,497	915	810	—
Middle						7,759	5,091	—	801	—
Lower						26,662	7,851	—	1,453	—
Stream estimate						35,077	13,434	[2]8,000	3,043	—
Funny Creek						1,616	1,037	615	503	1,239
1966:										
Sashin Creek:										
Upper									1,828	—
Middle									1,862	—
Lower									8,627	—
Stream estimate									12,346	—
Funny Creek									801	2,084

[1]The estimated populations of fish of a brood year at age I (second summer of life) include an average of 11% age II fish from the preceding brood year.
[2]Estimate of population from expansion of estimated populations in upper area and Funny Creek.

TABLE 17.—Mean stream discharge and percentage decrease in numbers of juvenile coho salmon between a first estimate (late June to late July) and a second estimate (mid-July to mid-August) in Sashin Creek, 1964-67.

Year	Mean stream discharge (m^3/s)	Decrease in population size	
		Fry	Fingerlings
1964	[1]1.70	71% (51,852 to 15,185)	[2]
1965	0.99	78% (20,355 to 4,546)	16% (4,581 to 3,836)
1966	0.82	62% (35,077 to 13,434)	45% (2,883 to 1,585)
1967	1.42	[3] (12,346)	[3] (3,043)

[1]Stream discharge data for August 1964 not measured. An estimate of mean stream discharge for the period was calculated from July 1964 stream discharge and rainfall data in conjunction with the August 1964 rainfall pattern.
[2]Size of fingerling population not estimated in 1964.
[3]First population estimate; second population estimate was not completed.

feeding area or refuge from undesirable conditions in Sashin Creek, such as competition or predation. Fall migration of juvenile coho salmon into small tributary streams in Oregon has been reported (Skeesick 1970).

Estimates of the number of coho salmon fry and fingerlings were used to construct curves depicting the changes in the sizes of the populations of three of the brood years studied (Figures 10, 11). Estimates of the total number of fry and fingerlings in Sashin Creek in early September 1966 are projected from estimates of population size obtained in the upper area and in Funny Creek. In these two study areas in early September the number of fry averaged 60% and the number of fingerlings 85% of their populations in late July. We assumed that these percentages pertained also to the lower and middle areas of Sashin Creek.

Survival and Instantaneous Mortality Rates

We compared survival and instantaneous mortality rates of juvenile coho salmon of three brood years by dividing their freshwater lives into the following five periods between the time of egg deposition and late in the second summer of life:

Period	*Time covered*
1	Egg deposition to just before emergence (mid-October to late March or early April).

TABLE 18.–Densities of juvenile coho salmon by brood year (1963-66)[1] on dates of population estimates in Sashin Creek and Funny Creek. Separate estimates are included for three areas of Sashin Creek.

Brood year and area	Density of fish (per square meter) on									
	12 July 1964	12 Aug. 1964	17 July 1965	1 Aug. 1965	11 Aug. 1965	27 June 1966	29 July 1966	8 Sept. 1966	23 July 1967	17 Aug. 1967
1963:										
Sashin Creek:										
Upper	—	—	0.16	—	0.15					
Middle	—	—	0.27	—	0.25					
Lower	—	—	0.31	—	0.26					
Stream estimate	3.13	0.92	0.28	—	0.23					
Funny Creek	—	—	—	1.93	1.26					
1964:										
Sashin Creek:										
Upper			0.74	—	0.06	0.10	0.13	0.12		
Middle			0.49	—	0.21	0.16	0.12	—		
Lower			1.83	—	0.43	0.19	0.07	—		
Stream estimate			1.23	—	0.27	0.17	0.10	[2]0.08		
Funny Creek			—	2.72	2.23	0.57	0.88	0.72		
1965:										
Sashin Creek:										
Upper						0.29	0.37	0.23	0.20	—
Middle						1.75	1.15	—	0.18	—
Lower						3.31	0.97	—	0.18	—
Stream estimate						2.12	0.81	[2]0.48	0.18	—
Funny Creek						3.66	2.35	1.39	1.14	2.81
1966:										
Sashin Creek:										
Upper									0.45	—
Middle									0.42	—
Lower									1.07	—
Stream estimate									0.75	—
Funny Creek									1.82	4.73

[1]The estimated populations of fish of a brood year at age I (second summer of life) include an average of 11% age II fish from the preceding brood year.
[2]Estimate of density calculated from population obtained from expansion of estimated populations in upper area and Funny Creek.

2 Just before emergence to first estimate of fry population (end of period 1 to late June or mid-July).

3 First to second estimate of fry population during first summer (end of period 2 to late July or mid-August).

4 Second estimate of fry population to first estimate of population as yearlings (end of period 3 to late June or mid-July of the following year).

5 First to second estimate of yearling population (end of period 4 to late July or mid-August).

Although the lengths of the corresponding periods for the three brood years are similar, they varied according to when the population estimates were made.

We compared the estimates of the population at the end of each of the five periods with the original population (potential egg deposition) to obtain percentage survival during nearly 2 yr of their freshwater life for the brood years 1963-65 (Table 19). Survival from potential egg deposition to just before fry emergence (period 1) was estimated to be 15%, 22%, and 26% (mean of 21%) for the 1963, 1964, and 1965 broods, respectively. Other investigators have found similar survival to emergence for coho salmon. A range in survival to emergence in terms of counted fry of 11.8% to 40.0% (mean of 21.0% and 26.5%) is reported for two tributaries of the Cowichan River, British Columbia (Pritchard 1947). Koski (1966) obtained survival values to fry emergence of 0% to 78% (mean of 27.1%) for individual redds of coho salmon in three streams tributary to Drift Creek. For Karymaisky Spring on Kamchatka, Semko (1954) reports survival to emergence of 0.8% to 21.4% (mean 10.6%).

TABLE 19.–Survival through five periods[1] in the freshwater life of three brood years of coho salmon in Sashin Creek, expressed as a percentage of potential egg deposition.

Brood year	Percentage survival through period				
	1	2	3	4	5
1963	14.66	3.55	1.04	0.28	0.23
1964	22.31	7.83	1.75	0.99	0.54
1965	25.71	10.02	3.84	0.77	—

[1]See text for explanation of time covered in each period.

Because the lengths of the five periods were not equal and a specific period was not the same length

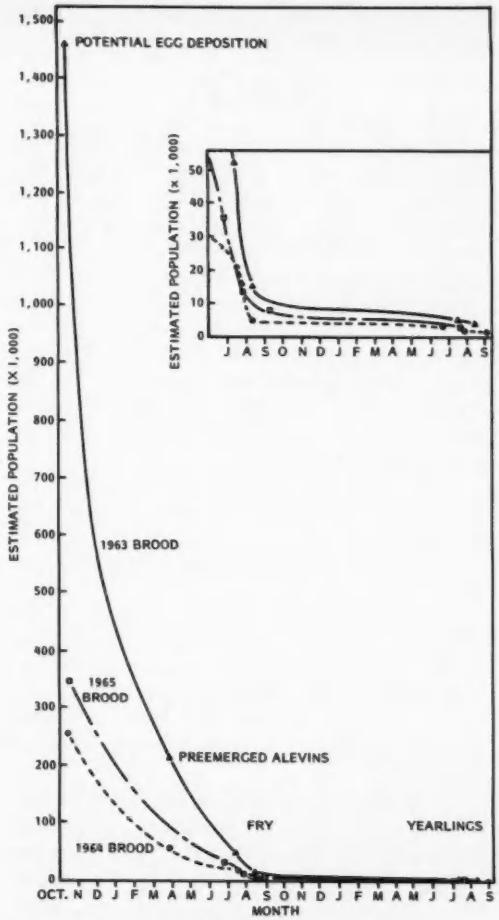
POTENTIAL EGG DEPOSITION
ESTIMATED POPULATION (X 1,000)
1963 BROOD
1965 BROOD
1964 BROOD
PREEMERGED ALEVINS
FRY
YEARLINGS
ESTIMATED POPULATION (x 1,000)
J A S O N D J F M A M J J A S
OCT. N D J F M A M J J A S O N D J F M A M J J A S
MONTH

FIGURE 10.—Estimated populations of juvenile coho salmon of three brood years, Sashin Creek, from potential egg deposition to late summer of second year. (Arithmetic plot.)

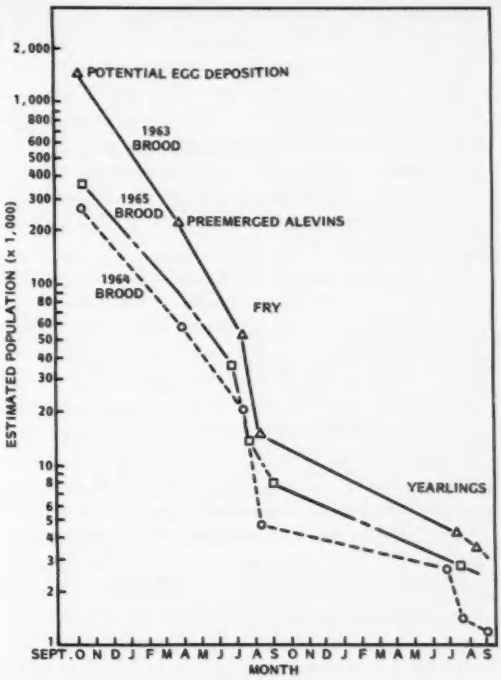
POTENTIAL EGG DEPOSITION
1963 BROOD
1965 BROOD
1964 BROOD
PREEMERGED ALEVINS
FRY
YEARLINGS
ESTIMATED POPULATION (x 1,000)
SEPT. O N D J F M A M J J A S O N D J F M A M J J A S
MONTH

FIGURE 11.—Estimated populations of juvenile coho salmon of three brood years, Sashin Creek, from potential egg deposition to late summer of second year. (Semilogarithmic plot to indicate mortality rate.)

TABLE 20.—Instantaneous mortality coefficients during five periods[1] in the freshwater life of three brood years of coho salmon in Sashin Creek.

Brood year	Instantaneous mortality coefficient in period				
	1	2	3	4	5
1963	0.37	0.38	1.23	0.12	0.25
1964	0.27	0.30	1.88	0.05	0.55
1965	0.25	0.32	0.87	0.14	—

[1]See text for explanation of time covered in each period.

for each of the three brood years, instantaneous mortality coefficients (Ricker 1958) were computed to compare mortality for the periods and years (Table 20). The equation for determining the instantaneous mortality coefficient,

$$M_{jn} = \frac{-\ln (S_{jn})}{t},$$

follows the notation of McNeil (1966), where t, the interval of time, is in months (one unit is equal to 1 mo); the symbol ln represents the natural logarithm; j is the brood year; and n is the study period. S_n is the survival within the nth period and is calculated from the formula,

$$S_1 \cdot S_2 \cdot \ldots \cdot S_n = S,$$

or

$$S_n = \frac{S}{S_1 \cdot S_2 \cdot \ldots \cdot S_{n-1}},$$

where S is survival through n study periods expressed as a percentage of potential egg deposition (Table 19).

Instantaneous mortality was higher through

periods 1 and 2 for the 1963 brood than for the 1964 and 1965 broods. We estimated that eggs of the 1963 brood were over four times as abundant as those of the 1965 brood and over five times as abundant as those of the 1964 brood. Resulting density-dependent factors such as superimposition of redds, selection of inferior redd sites, and emigration of fry from the stream because of lack of living space could be the cause of the higher initial mortality of the 1963 brood.

For all three broods the highest instantaneous mortality occurred in period 3—between the first and second population estimates of the first summer of life—during July and the first half of August (Table 20). Predation from fishes (both intraspecific and interspecific) is thought to be a major cause of this high mortality. In period 2 the fry live in the backwater and shallow edges of the stream where larger piscivorous fish do not regularly occur. During period 3 the fry move into deeper parts of the main channel where current is still relatively slow, but here larger fish occur and the fry may be more subject to predation.

Instantaneous mortality during the winter (period 4) was much less than that of the first summer. Predation probably was less during this period for two reasons: 1) in winter the feeding rate of cold-blooded predators is slowed, and 2) restricted access because of ice and snow and lowered activity and availability of the juvenile coho salmon combine to lessen the hunting success of warm-blooded predators.

Mortality increased during the second summer (period 5) but only to a third or less of the corresponding part of the first summer (period 3).

Some of the estimated mortality of fry and fingerlings might have been due to undetected emigration from the creek. When the fry weir or fyke nets were fished in summer (periods 3 and 5), however, only a few fry and fingerlings emigrated and the low mortality rate in period 4 also suggests that only a few fry emigrated in fall and winter. Some age I smolts probably migrated from the stream in the spring of period 4 in each of the 3 yr studied. The drop in population of a brood year due to age I smolt emigration is included as part of period 4 mortality. Age composition of smolts in 1965, 1966, and 1967 was not determined. The age composition of returning adults in 1966 and 1967 (25% and 29% age 3_2, respectively) indicates that some age I smolts emigrated in the spring of 1965 and 1966. In 1968 the smolts were sampled for age composition; about 500 yearling smolts migrated. Scale samples for age analysis were not collected from adults in 1968.

SUMMARY

The number of adult coho salmon that enter Sashin Creek varies from year to year. Coho salmon have been counted at the weir as they enter Sashin Creek each year since 1934, but this count has usually been incomplete.

Several methods were used to estimate coho salmon escapements to Sashin Creek for the years 1963-65 and 1967. These included weir counts, adults on spawning riffles, mean redd life, and marked-to-unmarked ratios of spawners. The last system produced the most accurate estimates, resulting in 916, 162, 221, and 370 salmon for the respective study years.

In the 4 yr that spawning ground studies were made, the density of coho salmon on the spawning grounds in Sashin Creek tended to be greater in the middle and lower study areas than in the upper area.

The effect of coho salmon spawning on the survival of pink salmon embryos was insignificant in 1965 relative to the population ratios of coho and pink salmon present. Significant numbers of pink salmon embryos might be killed if relatively large numbers of coho salmon utilized Sashin Creek for spawning.

The 4_3 age-group of coho salmon made up 78%, 59%, 64%, and 62% of the adults that returned to Sashin Creek in 1965, 1966, 1967, and 1969—higher percentages of this age group than reported for most other streams. In California, Oregon, Washington, and southern British Columbia, adult coho salmon are almost exclusively age 3_2. Studies of growth and scales of fry, fingerlings, and smolts and estimates of the population sizes of juveniles indicate that most coho salmon remain in Sashin Creek for two summers and winters.

In some years, substantial numbers of coho salmon fry enter the estuary of Sashin Creek shortly after emergence. These fry were tested and found to be able to survive in salinities encountered in the inner bay of the Little Port Walter estuary. However, analysis of scales of adult coho salmon returning to Sashin Creek revealed none that had migrated to the estuary at the fry stage, suggesting no fry (or at best very few) that migrate to the ocean survive to return as adults. This agrees with studies of other stocks of coho salmon.

Estimates of populations of fry in the early summer for the 4 yr studied ranged from about 12,000 to 52,000, and apparently varied directly with potential egg deposition of the brood year. However, by early in the second summer of freshwater life, the three broods studied had been reduced to a relatively narrow range of 3,000 to 4,500. Weir counts indicate 1,000 to 3,000 coho salmon smolts migrate from Sashin Creek each year.

The survival of coho salmon from potential egg deposition to just before the emergence of fry in Sashin Creek averaged 21%; this percentage is similar to survival reported for stocks from other areas in the eastern Pacific. Mortality of embryos and alevins was highest for the large 1963 brood, which suggests that some of the mortality before emergence was due to compensatory factors such as selection of inferior redd sites and superimposition of redds.

Highest mortality during the freshwater life of coho salmon from Sashin Creek occurred in July and early August of the first summer in all three broods studied. The lowest mortality occurred over winter.

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LITERATURE CITED

ALLEN, G. H.
1958. Notes on the fecundity of silver salmon (*Oncorhynchus kisutch*). Prog. Fish-Cult. 20:163-169.

ANDREWS, R. E.
1961. Inventory and cataloging of the sport fish waters in the Cook Inlet and Copper River drainages. Alaska Dep. Fish Game, Sport Fish Div., 1960-61 Dingell-Johnson Proj. Rep. 2:47-55.
1962. Inventory and cataloging of sport fish and sport fish waters of the Cook Inlet drainages. Alaska Dep. Fish Game, Sport Fish Div., 1961-62 Dingell-Johnson Proj. Rep. 3:221-225.

ARMSTRONG, R. H.
1970. Age, food, and migration of Dolly Varden smolts in southeastern Alaska. J. Fish. Res. Board Can. 27:991-1004.

BRIGGS, J. C.
1953. The behavior and reproduction of salmonid fishes in a small coastal stream. Calif. Dep. Fish Game, Fish Bull. 94, 62 p.

CHAMBERLAIN, F. M.
1907. Some observations on salmon and trout in Alaska. [U.S.] Bur. Fish., Rep. Comm. Fish. 1906. Doc. 627, 112 p.

CHAPMAN, D. W.
1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. J. Fish. Res. Board Can. 19:1047-1080.
1965. Net production of juvenile coho salmon in three Oregon streams. Trans. Am. Fish. Soc. 94:40-52.

CONTE, F. P., H. H. WAGNER, J. FESSLER, AND C. GNOSE.
1966. Development of osmotic and ionic regulation in juvenile coho salmon *Oncorhynchus kisutch*. Comp. Biochem. Physiol. 18:1-15.

DRUCKER, B.
1972. Some life history characteristics of coho salmon of the Karluk River system, Kodiak Island, Alaska. Fish. Bull., U.S. 70:79-94.

ENGEL, L. J.
1965. Egg take investigations in Cook Inlet drainage and Prince William Sound. Alaska Dep. Fish Game, Sport Fish Div., 1964-65 Dingell-Johnson Proj. Rep. 6:155-163.
1966. Egg-take investigation in Cook Inlet drainage and Prince William Sound. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1965-66 Prog. Rep. 7:109-116.
1967. Egg take investigation in Cook Inlet drainage and Prince William Sound. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1966-67 Prog. Rep. 8:111-116.

FOERSTER, R. E.
1944. Appendix IV. Report for 1943 of the Pacific Biological Station, Nanaimo, B.C. Annu. Rep. Fish. Res. Board Can. 1943:22-26.
1955. The Pacific salmon (genus *Oncorhynchus*) of the Canadian Pacific coast, with particular reference to their occurrence in or near fresh water. Int. North Pac. Fish. Comm., Bull. 1:1-56.

FOERSTER, R. E., AND A. L. PRITCHARD.
1936. The egg content of Pacific salmon. Biol. Board Can., Prog. Rep. Pac. Biol. Stn. Pac. Fish. Exper. Stn. 28:3-5.

FOERSTER, R. E., AND W. E. RICKER.
1953. The coho salmon of Cultus Lake and Sweltzer Creek. J. Fish. Res. Board Can. 10:293-319.

GARRISON, R. L.
1965. Coho salmon smolts in ninety days. Prog. Fish-Cult. 27:219-220.

GILBERT, C. H.
1913. Age at maturity of the Pacific coast salmon of the genus *Oncorhynchus*. Bull. [U.S.] Bur. Fish. 32:1-22. (Doc. 767.)
1922. The salmon of the Yukon River. Bull. [U.S.] Bur. Fish. 38:317-332. (Doc. 928.)

GODFREY, H.
1965. Salmon of the North Pacific Ocean—Part IX, Coho, chinook and masu salmon in offshore waters. 1. Coho salmon in offshore waters. Int. North Pac. Fish. Comm., Bull. 16:1-39.

GRIBANOV, V. I.
1948. The coho salmon (*Oncorhynchus kisutch* Walbaum)—a biological sketch. Izv. Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 28:43-101. (Fish. Res. Board Can. Transl. Ser. 370, 83 p.)

HUNTER, J. G.
1948. Natural propagation of salmon in the central coastal

area of British Columbia. Fish. Res. Board Can., Prog. Rep. Pac. Coast Stn. 77:105-106.

1949. Natural propagation of salmon in the central coastal area of British Columbia. II. The 1948 run. Fish. Res. Board Can., Prog. Rep. Pac. Coast Stn. 79:33-34.

INTERNATIONAL NORTH PACIFIC FISHERIES COMMISSION.

1962. The exploitation, scientific investigation and management of salmon (genus *Oncorhynchus*) stocks on the Pacific coast of the United States in relation to the abstention provisions of the North Pacific Fisheries Convention. Int. North Pac. Fish. Comm., Bull. 10, 160 p.

KOSKI, K. V.

1966. The survival of coho salmon (*Oncorhynchus kisutch*) from egg deposition to emergence in three Oregon coastal streams. M.S. Thesis, Oregon State Univ., Corvallis, 84 p.

KUBIK, S.

1967. Population studies of anadromous species with emphasis on upper Cook Inlet drainage. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1966-67 Prog. Rep. 8:117-128.

KUZNETSOV, I. I.

1928. Some observations on spawning of the Amur and Kamchatka salmons. Izv. Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 2. (Fish. Res. Board Can. Transl. Ser. 22, 9 p.)

LAWLER, R. E.

1963. Silver salmon egg taking investigations in Cook Inlet drainage. Alaska Dep. Fish Game, Sport Fish. Div., 1962-63 Dingell-Johnson Proj. Rep. 4:161-173.

1964. Egg take investigation in Cook Inlet drainage and Prince William Sound. Alaska Dep. Fish Game, Sport Fish Div., 1963-64 Dingell-Johnson Proj. Rep. 5:123-132.

LOGAN, S. M.

1963. Silver salmon studies in the Resurrection Bay area. Alaska Dep. Fish Game, Sport Fish Div., 1962-63 Dingell-Johnson Proj. Rep. 4:175-194.

1968. Silver salmon studies in the Resurrection Bay area. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1967-68 Prog. Rep. 9:117-134.

MARR, J. C.

1943. Age, length, and weight studies of three species of Columbia River salmon (*Oncorhynchus keta*, *O. gorbuscha*, *O. kisutch*). Stanford Ichthyol. Bull. 2:157-197.

MARRIOTT, R. A.

1968. Inventory and cataloging of the sport fish and sport fish waters in southwest Alaska. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1967-68 Prog. Rep. 9:81-93.

MCGINNIS, D.

1966. Inventory, cataloging and population sampling of the sport fish and sport fish waters of the Cook Inlet drainage. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1965-66 Prog. Rep. 7:155-169.

MCNEILL, W. J.

1964. A method of measuring mortality of pink salmon eggs and larvae. U.S. Fish. Wildl. Serv., Fish. Bull. 63:575-588.

1966. Distribution of spawning pink salmon in Sashin Creek, southeastern Alaska, and survival of their progeny. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 538, 12 p.

MEEHAN, W. R., AND D. B. SINIFF.

1962. A study of the downstream migrations of anadromous fishes in the Taku River, Alaska. Trans. Am. Fish. Soc. 91:399-407.

MERRELL, T. R., JR.

1962. Freshwater survival of pink salmon at Sashin Creek, Alaska. *In* N. J. Wilimovsky (editor), Symposium on pink salmon, p. 59-72. Univ. B.C., H. R. MacMillan Lect. Fish., Vancouver.

NEAVE, F.

1948. Fecundity and mortality in Pacific salmon. Trans. R. Soc. Can., Ser. 3, Sect. 5, 42:97-105.

OLSON, J. M., AND W. J. MCNEIL.

1967. Research on pink salmon at Little Port Walter, Alaska, 1934-64. U.S. Fish Wildl. Serv., Data Rep. 17, 301 p. on 5 microfiche.

OTTO, R. G.

1971. Effects of salinity on the survival and growth of pre-smolt coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 28:343-349.

PARKER, R. R., AND R. E. VINCENT.

[1956]. Progress report on research studies at the Kitoi Bay Research Station. Alaska Fish. Board and Alaska Dep. Fish. 1955 Annu Rep. 1957:25-67.

POWERS, C. F.

1963. Some aspects of the oceanography of Little Port Walter estuary, Baranof Island, Alaska. U.S. Fish Wildl. Serv., Fish. Bull. 63:143-164.

PRITCHARD, A. L.

1940. Studies on the age of the coho salmon (*Oncorhynchus kisutch*) and the spring salmon (*Oncorhynchus tshawytscha*) in British Columbia. Trans. R. Soc. Can., Ser. 3, Sec. 5, 34:99-120.

1947. Efficiency of natural propagation of Pacific salmon. Can. Fish Cult. 1:22-26.

REDICK, R. R.

1968. Population studies of anadromous fish populations–southwestern Kenai Peninsula and Kachemak Bay. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1967-68 Prog. Rep. 9:135-155.

RICKER, W. E.

1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can., Bull. 119, 300 p.

ROBSON, D. S., AND H. A. REGIER.

1964. Sample size in Petersen mark-recapture experiments. Trans. Am. Fish. Soc. 93:215-226.

1968. Estimation of population number and mortality rates. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 124-158. IBP (Int. Biol. Programme)., Handb. 3.

ROUNSEFELL, G. A.

1957. Fecundity of North American Salmonidae. U.S. Fish Wildl. Serv., Fish. Bull. 57:451-468.

SALO, E. O., AND W. H. BAYLIFF.

1958. Artificial and natural production of silver salmon, *Oncorhynchus kisutch*, at Minter Creek, Washington. Wash. Dep. Fish., Res. Bull. 4, 76 p.

SEMKO, R. S.

1954. The stocks of west Kamchatka salmon and their commercial utilization. Izv. Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 41:3-109. (Fish. Res. Board Can. Transl. Ser. 288, 131 p.)

SHAPOVALOV, L., AND A. C. TAFT.

1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. Calif. Dep. Fish Game, Fish Bull. 98, 375 p.

SKEESICK, D. G.
1970. The fall immigration of juvenile coho salmon into a small tributary. Oreg. Fish Comm. Res. Rep. 2:90-95.

SMIRNOV, A. I.
1960. The characteristics of the biology of reproduction and development of the coho *Oncorhynchus kisutch* (Walbaum). Vestn. Mosk. Univ., Ser. VI, Biol. Pochv. 1960(1):9-19. (Fish. Res. Board Can. Transl. Ser. 287.)

SMOKER, W. A.
1953. Stream flow and silver salmon production in western Washington. Wash. Dep. Fish. Fish. Res. Pap. 1(1):5-12.
[1957.] Silver salmon research. Alaska Fish. Board and Alaska Dep. Fish. 1956 Annu. Rep. 8:42-46.

SNEDECOR, G. W.
1956. Statistical methods. 5th ed. Iowa State Univ. Press, Ames, 534 p.

U.S. GEOLOGICAL SURVEY.
1972. Water resources data for Alaska, 1968. Part 1. Surface water records. U.S. Dep. Inter. Geol. Surv., Water Res. Div., 155 p.

VAN HULLE, F. D.
1970. Inventory and cataloging of the sport fish and sport fish waters in southwest Alaska. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1969-70 Prog. Rep. 11:47-63.
1971. Inventory and cataloging of the sport fish and sport fish waters in southwest Alaska. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1970-71 Prog. Rep. 12:29-51.

WALLIS, J.
1967. Salmonid rearing and migration study—Fire Lake system and Fort Richardson cooling pond. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1966-67 Prog. Rep. 8:129-152.
1968. Salmonid rearing and migration study—Fire Lake system and Ft. Richardson and Elmendorf rearing ponds. Alaska Dep. Fish Game, Sport Fish Div., Fed. Aid Fish Restoration, 1967-68 Prog. Rep. 9:173-191.

WICKETT, W. P.
1951. The coho salmon population of Nile Creek. Fish. Res. Board Can., Prog. Rep. Pac. Coast Stn. 89:88-89.

WILLIS, R. A.
1954. The length of time that silver salmon spent before death on the spawning grounds at Spring Creek, Wilson River, in 1951-52. Oreg. Fish Comm. Res. Briefs 5:27-31.

VERTICAL DISTRIBUTION AND DIEL MIGRATION OF EUPHAUSIIDS IN THE CENTRAL REGION OF THE CALIFORNIA CURRENT

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ABSTRACT

The density, vertical range, and diel movement of total zooplankton and euphausiid populations in the central region of the California Current were determined during a period of coastal upwelling, July-August 1970. Collections were made along four transects with opening-closing Bongo nets towed through 50- to 100-m intervals in the upper 800 m. Four- to nine-depth intervals at 13 day-night stations were sampled. Twenty euphausiid species from seven genera were identified from 124 hauls.

Zooplankton assemblages in the nearshore regions differed from those farther offshore in having a larger biomass as well as a smaller number and higher density of several species. Diel vertical movement among euphausiid populations, particularly *Euphausia pacifica*, tended to be more pronounced in offshore waters. This behavior suggests that, although assemblages of zooplankton are strongly structured by physical factors, some species alter their vertical distribution and diel migration, presumably in response to the prevailing food supply.

Since 1949 an intensive plankton sampling program has been conducted in the California Current under the auspices of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). These surveys, concentrating on the distribution and density of pelagic organisms in the upper 150 m, have revealed abundance and dispersion patterns of zooplankton which are related to annual and seasonal changes in hydrographic conditions (Brinton 1960, 1962a; Thrailkill 1963; Fleminger 1964, 1967; Alvariño 1965; McGowan 1967; Berner 1967; Isaacs et al. 1969). Within a given year, varying proportions of zooplankton assemblages typical of any one of several water masses are likely to be present (Berner 1957; Bieri 1959; Brinton 1962b; Johnson and Brinton 1963; Cushing 1971). Seasonal hydrographic fluctuations near the coastal boundary of the current act to further transform the numbers and types of pelagic species that develop. For example, the eutrophic environment produced by coastal upwelling during the spring and summer months is characterized by a much higher biomass and lower species diversity than the more oligotrophic, offshore portion of the current (Frolander 1962; Hebard 1966; Laurs 1967; Longhurst 1967; Pieper 1967).

Considerably less attention has been given to the vertical distribution of zooplankton in this current principally because it is difficult, time consuming, and costly to repeatedly sample discrete depths. The scope of this study was to describe the vertical distribution and diel migration of zooplankton, particularly euphausiids, in nearshore and offshore oceanic regions of the central California Current during a period when coastal upwelling was well developed. The samples were collected in the summer of 1970 on two cruises, Stanford Oceanographic Expedition (SOE) cruise 22 and CalCOFI cruise 7008.

DESCRIPTION OF THE ENVIRONMENT

The California Current is a blend of water masses (Subarctic, North Pacific Drift, Central, and Equatorial) and is therefore an extremely variable environment (Reid et al. 1958; McGowan 1971). It flows southward throughout the year with an average velocity of less than 0.5 knot. The boundaries of this transitional water are between lat. 48° and 23°N and extend to 700 km (long. 130°W) from the coast. Between depths of 200 and 400 m, a subsurface countercurrent flows northward at about 0.5 knot from Baja California to Cape Mendocino (Kin'dyushov 1970).

Near the coast, hydrographic fluctuations in this current have been separated into seasonal periods of divergence (upwelling), relaxation (oceanic), and convergence (downwelling) (Bolin and Abbott

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1963; Dodimead et al. 1963). From March to August, the force of the prevailing northerly winds and the earth's rotation cause the southerly flowing surface waters, within 100 km of the shore, to move away from the coast (Yoshida 1955). This displaced water is replaced by cooler, more saline, nutrient-rich water upwelled from deeper regions, providing favorable conditions for high rates of primary production. In the central part of this current, the upwelling period is considered to begin and end with the shifting of the 9°C isotherm above and below the 100-m level (Barham 1957).

The northerly winds subside from September to November and surface water temperatures increase, resulting in the formation of a strong thermocline in the upper 50 m. During this surface-warmed period, in the absence of upwelling, tongues of offshore, oceanic water of the California Current may reach the coast. Where this occurs there is probably considerable mixing of oceanic and neritic planktonic communities (e.g., see Longhurst 1967).

When southerly winds prevail, in the period from December to February, a northerly flowing, coastal countercurrent (Davidson Current) may develop. Surface water converges toward the coast and disrupts the stratification characteristic of the surface-warmed water period. Vertical eddy circulation results, promoting the overturn, mixing, and downwelling of warm, lower salinity, nutrient-poor surface waters. This mixed water period can be characterized by a temperature gradient of less than 1°C in the upper 50 m.

The environments sampled at the shoreward and seaward stations in the summer of 1970 differed in several ways. Physical and chemical features relating to phytoplankton studies during the SOE cruise are presented in Malone (1971). These and other hydrographic features in the upper 800 m at each station are tabulated and discussed in Youngbluth (1973). By way of summary, it was clear from the low temperatures and high salinities and the shoreward elevation of nitrate isopleths that upwelling conditions prevailed near the coast. Chlorophyll-*a* values in the upper 150 m decreased with increasing distances from shore, 2.1-0.5 mg/m^3. The photic zone was usually deeper at the seaward stations, ranging from 55 m in coastal regions to 105 m at the western edge of the transects. The depth of the thermocline was shallower nearshore and deeper offshore, ranging from 5 to 40 m, respectively. The largest temperature difference between the thermocline and 150 m was about 4°C. At depths below 150 m, temperatures differed by 2°C or less among stations.

Temperature-salinity (T-S) curves from each station were compared to two different schemes (Youngbluth 1973). First, the data, when plotted with T-S relationships that characterize the percent mixing between waters near the northern and southern limits of the California Current (Okutani and McGowan 1969), indicated that between 150 and 800 m 70-100% northern water was present. The small percentage of southern water was most noticeable at the intermediate and nearshore stations of the southern transect. Second, the data, when contrasted with T-S curves that distinguish water masses, revealed that samples below 250 m were collected in North Pacific Intermediate water.

MATERIALS AND METHODS

Zooplankton samples were collected with opening-closing Bongo nets of 0.333-mm mesh and cod ends with 0.222-mm mesh (McGowan and Brown 1966). At nearly all stations, shallow and mid-water casts were made, within 3 h of midday and midnight at nearly the same location (Table 1). Shallow tows were taken with a single frame (SOE) or with four frames (CalCOFI) in the upper 150-200 m. Three (SOE) or four (CalCOFI) frames were used on mid-water hauls between 200 and 600

TABLE 1.—The date and position of Bongo net tows.

Cruise	Date 1970	Station	Position Lat. N	Position Long. W
SOE 22	27 July 28 July	9	37°09′	124°24′
	29 July 30 July	16	37°15′	128°45′
	31 July 1 Aug.	25	36°39′	130°53′
	3 Aug. 4 Aug.	39	39°54′	129°58′
	5 Aug. 6 Aug.	47	39°53′	127°48′
	7 Aug. 8 Aug.	56	39°53′	125°48′
	16 Aug. 18 Aug.	68	43°49′	125°49′
	19 Aug.	74	43°55′	128°03′
	20 Aug.	81	43°32′	129°58′
CalCOFI 7008	27 Aug. 28 Aug.	70.75	35°23′	123°27′
	20 Aug. 21 Aug.	50.80	38°40′	126°21′
	18 Aug. 19 Aug.	50.110	37°40′	128°33′
	16 Aug. 17 Aug.	50.140	36°40′	130°44′

m. Depth intervals of about 100 m were sampled. A single frame (CalCOFI) was employed at depths from 600 to 800 m. The nets were hauled along a single oblique path (all CalCOFI and shallow SOE casts) or undulated obliquely through the depth intervals sampled (all mid-water SOE casts). Each point on the graphs representing these data is the middepth of the water column sampled.

The strata sampled were recorded with a Benthos depth-time device attached a few meters below the bottom frame. Vessel speed during the tows ranged between 2 and 2.5 knots (3.7 and 4.6 km/h) and was regulated to maintain a wire angle of approximately 50°. Mean volumes of 619 m^3 (SOE shallow tows), 957 m^3 (SOE mid-water tows), and 546 m^3 (all CalCOFI tows) were filtered. All data were standardized to a volume of 1,000 m^3, assuming 100% filtration efficiency. Clogging of net apertures was observed only in the uppermost nets at the nearshore stations on the CalCOFI cruise.

The samples were preserved in 5% Formalin[2] solution buffered to pH 7.6. All organisms longer than 2 cm were removed from the sample and wet weights were determined after draining the remaining portion on a 0.222-mm mesh screen and blotting it on absorbent paper for 20 min. Duplicate estimates varied by an average of 6%.

The larvae (furcilia), juveniles (postlarvae and immatures), and adults (sexually mature) of all euphausiid species were studied. All individuals of the less abundant species were identified and counted. The densities of the more numerous species were determined from subsamples made with a modified Folsom Plankton Splitter. The average number of specimens examined in the subsamples was about 300. Duplicate counts were compared with each other by calculating a Percent Similarity Index (Whittaker 1952).

If the index indicated at least 80% agreement between the first two replicates, no other counts were made. Occasionally a third count was necessary.

The taxonomy of adult euphausiids follows Boden et al. (1955). Identification of certain difficult groups, e.g., *Nematoscelis* spp., *Thysanoessa* spp., and all larvae were verified by E. Brinton, T. Antezana, and K. Gopalakrishnan at the Scripps Institution of Oceanography. When specimens lacked some of the usual key characters, general body form and eye size, shape, and color were used to distinguish the species.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Sampling Variability Between Cruises

Samples were collected along four transects. The stations ranged from 130 to 693 km off the coast (Figure 1). During the CalCOFI cruise, a smaller average volume of water was filtered by each net. Presumably this smaller volume could have introduced some bias by reducing species diversity and abundance estimates. Comparisons of the results from each cruise indicate that, except for three rarely caught species: 1) the number of euphausiid species collected was identical and 2) the order of species abundances was quite similar on each cruise. Biomass values of total zooplankton tended to be larger at the seaward stations during the CalCOFI cruise. This difference is most likely related to the greater number and narrower, vertical width of the tows taken during this cruise, and, to some extent, growth and development of each life stage as well

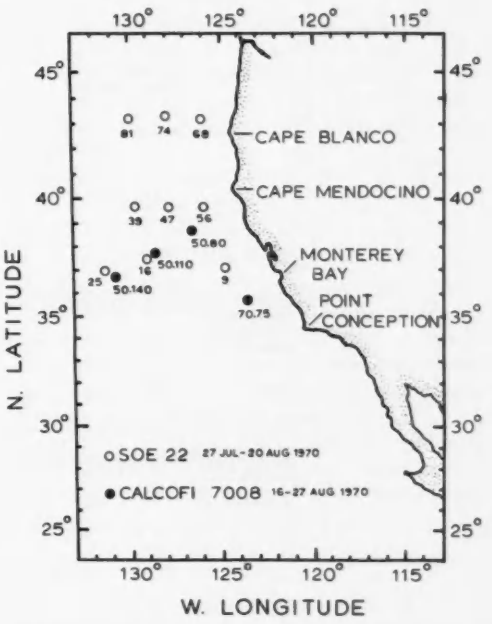

FIGURE 1.—Positions of the day-night stations in the central portion of the California Current.

as offshore transport of the more numerous species observed in nearshore waters.

Distribution of Zooplankton Biomass

The standing stock of zooplankton was highest at the nearshore stations and decreased with distances seaward. The largest and smallest biomass values occurred along the southern transect and corresponded with high and low phytoplankton stocks, respectively (Malone 1971).

Zooplankton were concentrated in the upper 100-150 m at most stations, particularly in the mixed layer (ca. 0-40 m). Densities ranged from 10 to 580 g wet wt/1,000 m^3 (Figure 2). Below 100-150 m, the amount of zooplankton at approximately 100-m intervals was generally between 25 and 150 g wet wt/1,000 m^3. Diel fluctuations in biomass were greatest in the surface water (0-150 m)

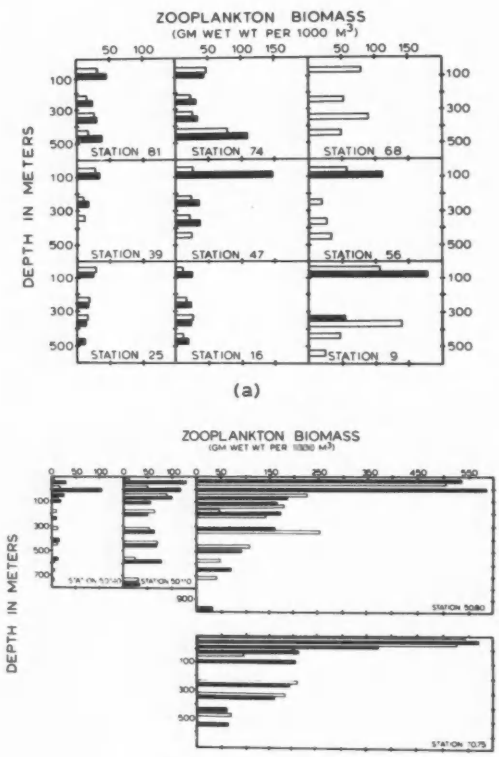

FIGURE 2.—The vertical distribution of zooplankton biomass. Clear bars indicate day samples; dark bars designate night samples. (a) SOE cruise 22 and (b) CalCOFI cruise 7008.

increasing at night by factors of 1.2-8. At two nearshore stations, CalCOFI 50.80 and 70.75, large quantities of phytoplankton clogged net meshes in the upper 50 m and prevented any quantitative comparison of day and night catches. Below 150 m, a small but consistent increase in biomass was usually observed at night ($P = 0.20$, Sign Test). During the day, at some intervals between 250 and 400 m, biomass was equal to or slightly greater than concentrations in the upper 150 m.

Diversity, Density, and Distribution of Euphausiid Species

Twenty species of euphausiids distributed among seven genera were identified. Thirteen species occurred frequently enough and in sufficient numbers to allow descriptions of their vertical distribution. In the upper 150 m, 8 species formed 50% of the total abundance and 12 made up 90%. Nine species were found at more than half the stations. In the total water column sampled (ca. 0-700 m), 6 and 11 species composed 50 and 90% of the total species abundance. At most stations one or two species were numerically dominant.

The distributions of euphausiids at midday and midnight are discussed in the following paragraphs. Only examples of a few species are illustrated to represent the major patterns observed since a large number of profiles were derived from the data for all the species collected at each station (Youngbluth 1973). In many cases, diurnal changes in vertical distributions were obscured either by patchiness or avoidance or incomplete sampling due to gear failure or foul weather. This account is thus a composite description of the data from all stations.

Euphausia

Four species of *Euphausia* were taken—*E. pacifica*, *E. recurva*, *E. gibboides*, and *E. mutica*. With the exception of *E. pacifica*, these species were only abundant at the offshore stations along the southern transects (SOE 16, 25; CalCOFI 50.110). In this region densities of each species usually ranged between 10 and 200/1,000 m^3. Juveniles and larvae were often more than twice as numerous as adults. The daytime habitat of *E. mutica* larvae was between 100 and 400 m. Juveniles of this species were found only in one haul which sampled from 400 to 500 m (SOE 16). *Euphausia gibboides* and *E. recurva* were collected

somewhat deeper, 250-350 m and 400-600 m, respectively. At night all stages of these species migrated into the upper 100 m. *Euphausia mutica* and *E. recurva* appeared in the upper 50 m, whereas *E. gibboides* was more widely distributed with most of the population between 50 and 250 m (e.g., CalCOFI 50.140).

The relative abundance, vertical distribution, and diel migration of *E. pacifica* varied with distance from the coast (Figure 3). Data from all stations are illustrated to show the number of patterns exhibited by this species. Larvae and juveniles tended to occupy a much wider vertical range in nearshore waters. The bulk of the larvae was usually found in the upper 150 m day and night. The single exception to this pattern was observed at CalCOFI 70.75 where the larvae were abundant at 250 m throughout the day and in very large numbers in the upper 100 m at night. Juveniles were numerous in the surface waters as well as at depths to 450 m. The adult phase was frequently most abundant between 200 and 400 m during the daytime. Offshore, during the day, densities of this species were reduced, adults were rarely collected, and populations occurred at deeper, narrower intervals. At night, both nearshore and offshore, only some members of each stage migrated to the surface waters from depths of 250-450 m. The general features of the geographical distribution of this species in the central regions of the California Current agree with observations by Brinton (1962b, 1967); the vertical dimensions are more detailed.

Tessarabrachion

The only species of this genus, *T. oculatus* was frequently found in small numbers, i.e., 10-20/1,000 m^3. Juveniles and adults of this characteristic subarctic species were common and occurred between 70 and 500 m. Somewhat greater numbers were collected at night. The larvae tended to remain closer to the surface, i.e., from 70 to 200 m (SOE 74; CalCOFI 50:110), than juveniles and adults which were usually found between 200 and 400 m. Thus, this species inhabits a wide depth interval below the thermocline regardless of the time of day.

Thysanopoda

Three species of *Thysanopoda* were collected–*T. aequalis*, *T. acutifrons*, and *T. egregia*. Very few specimens of these species were taken. Larvae of *T. aequalis*, a species typical of central water masses, were found in the upper 200 m at the offshore stations of the southernmost transect. Adults, found only at night at the same stations, were collected above 300 m. Larvae of *T. acutifrons* were not observed. One juvenile and one adult were taken during the day between 400 and 500 m at different offshore stations. At night a total of 11 adults and 2 juveniles were caught between 200 and 500 m (SOE 16, 74; CalCOFI 50.110, 50.140). One to four larvae of *T. egregia* were collected between 50 and 450 m at nearly all but the most northern stations.

Thysanoessa

Three species of *Thysanoessa* were found–*T. spinifera*, *T. gregaria*, and *T. longipes*. *Thysanoessa spinifera* was only collected near the coast, most frequently in the upper 150 m. Small densities of juveniles, the most abundant stage, were present in tows from 150 to 350 m (CalCOFI 50.80, 70.75). Adults were not collected. The preponderance of *T. spinifera* in the neritic environment has been noticed previously (Brinton 1962a; Hebard 1966). Diel changes in the vertical distribution of juveniles indicate that perhaps some members of this phase migrated into the upper 100 m at night (Figure 4a). These data support other studies that have suggested this species is a diel migrant (Regan 1968; Day 1971; Alton and Blackburn 1972).

Thysanoessa gregaria occurred at all but one location (SOE 68). This species was found most often in the upper 150 m, although it ranged to 300 m. Juvenile phases dominated the catches during the SOE cruise. All stages were abundant among the CalCOFI samples gathered 2 wk later. Densities were greater along the southern transects. From 50 to 500 individuals/1,000 m^3 were recorded within depth intervals where the largest concentrations occurred. Larvae usually resided in the upper 50 m. Juveniles and adults were numerous between 50 and 200 m and often 3-10 times more numerous in the night tows. These data suggest that the older stages probably avoided the sampling gear during the day. At one station (CalCOFI 70.75), all stages of *T. gregaria* were observed only in the upper 20 m during the day. At night this species ranged to 400 m with the largest densities occurring between 60 and 100 m and no specimens were collected in the upper 30 m. These

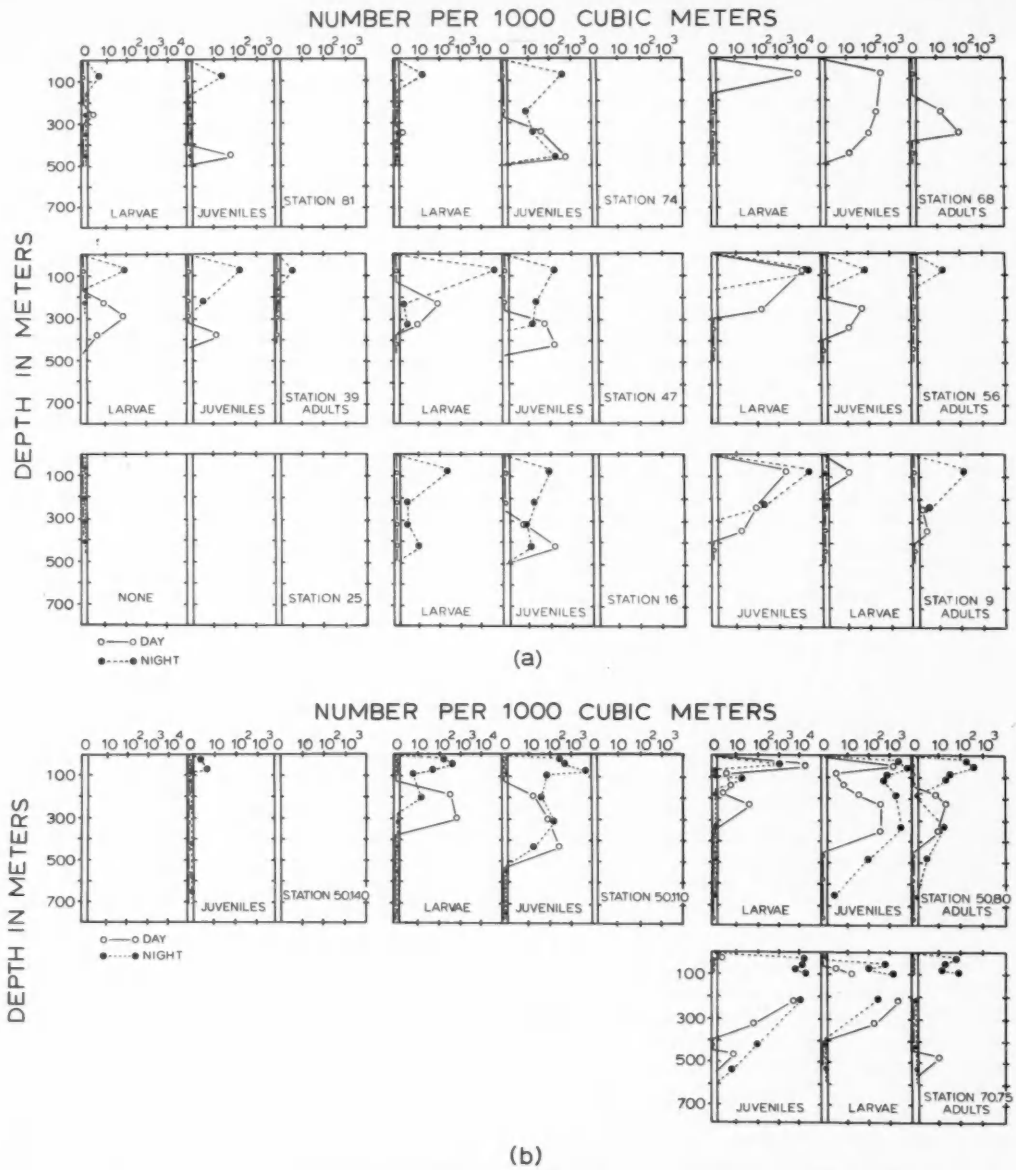

FIGURE 3.—The vertical distribution of *Euphausia pacifica* according to stage of development. (a) SOE cruise 22 and (b) CalCOFI cruise 7008.

observations indicate this species can be contagiously dispersed.

All phases of *T. longipes* (unspined form) were collected in the upper 150 m. Juveniles and adults were also abundant between 200 and 800 m. Portions of these older populations appeared to migrate toward the surface at night at several stations (SOE 9, 74, 81; CalCOFI 50.80, 50.110) (Figure 4b). The vertical range of this species agrees with observations by Brinton (1962b) and

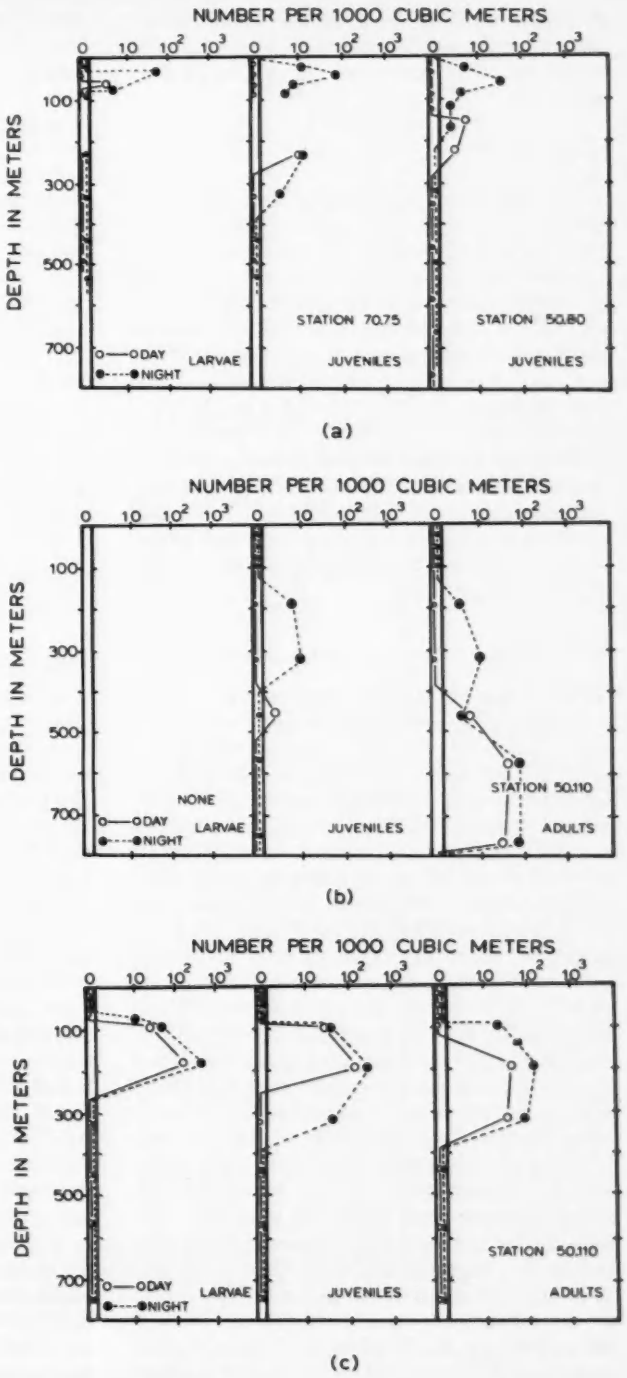

FIGURE 4.—Examples for the vertical distribution of (a) *Thysanoessa spinifera*, (b) *Thysanoessa longipes*, and (c) *Stylocheiron longicorne* according to stage of development.

Ponomareva (1963). The abundance in subsurface waters and the possible migratory behavior of this unspined form have not been documented previously.

Nematoscelis

Two species of *Nematoscelis* were taken–*N. tenella* and *N. difficilis*. *Nematoscelis tenella* was collected at only one day-night station (SOE 16). The few adults and juveniles caught, 2-13/1,000 m^3, were found between 400 and 500 m during the day and 0 and 250 m at night. *Nematoscelis difficilis* occurred between the surface and 450 m at all but one station (SOE 25). This species was more abundant near the coast along the CalCOFI transect. Densities ranging in the hundreds per 1,000 m^3 at nearshore stations were an order of magnitude larger than concentrations among samples from waters farther offshore. Larvae and most juveniles were taken only in the upper 100 m. Adults were more abundant between 100 and 300 m, particularly at night.

Stylocheiron

Five species of this genus were found–*S. affine*, *S. longicorne*, *S. maximum*, *S. elegatum*, and *S. abbreviatum*. These species occupied similar depth intervals day and night although each species tended to inhabit a separate portion of the water column. *Stylocheiron affine* occurred only along the southern transect. All stages were collected between 40 and 135 m and primarily at the most offshore stations where densities of 60-150/1,000 m^3 were recorded (SOE 25; CalCOFI 50.140). Each stage was often more abundant in the night samples. *Stylocheiron longicorne*, the most abundant species of this genus, ranged between 70 and 350 m, but the bulk of the populations were within the 150- to 250-m interval (Figure 4c). More specimens were usually caught at night. *Stylocheiron maximum* occurred in low densities at every station, i.e., 5-40/1,000 m^3. Larvae and juveniles of this species were found most often between 70 and 200 m. Adults were generally deeper, ranging from 200 to 400 m. Differences between day and night distributions indicate that this species migrated less than 100 m, if at all. Very small densities of *S. elongatum*, 1-27/1,000 m^3, were observed at the offshore stations between 200 and 600 m. A few adults of *S. abbreviatum* were found along the southern transect of the SOE cruise. Four individuals were collected in the upper 150 m at stations well offshore (SOE 25, 39) and one between 300 and 400 m nearshore (SOE 9).

Nematobrachion

Two species of *Nematobrachion* were found–*N. boopis* and *N. flexipes*. One to two individuals of *N. boopis*, mostly juveniles, were taken between 300 and 500 m and only during the day at a few, southern stations (SOE 9; CalCOFI 70.75, 50.140). *Nematobrachion flexipes* occurred at all but one station (SOE 68). Small concentrations, usually 1-30/1,000 m^3 but ranging up to 69/1,000 m^3, were found regardless of the time of day. Juveniles were often the most numerous stage. This species was frequently encountered at 200-500 m during the day. At night specimens were collected from 450 m to the surface with most of a population in the upper 150 m.

PATTERNS OF ABUNDANCE, VERTICAL DISTRIBUTION, AND DIEL MIGRATION

The abundance and vertical distribution of the more numerous euphausiid species in the upper 500-700 m differed in relation to distance from shore, longitudinal position in the area sampled, and vertical ranges occupied during a given day. The largest densities of euphausiids occurred near the coast (Table 2). Among the nearshore stations (ca. 100-150 km from the coast) *E. pacifica* was the numerically dominant euphausiid day and night, composing 75-90% of all species observed. At intermediate distances from the coast (ca. 300 km), *E. pacifica* was less abundant, making up 36-60% of the species collected, but still ranked first except in the north (SOE 74) where *Thysanoessa longipes* formed 69% of the day catch. Other euphausiid species constituting 15-30% of the total number included *S. longicorne*, *E. gibboides*, *T. gregaria*, and *T. longipes*. At stations farthest offshore (ca. 600-700 km) along the southern transects, *T. gregaria* and *S. longicorne* were the most abundant species, forming 75% of the total during the day. At night, larger numbers of *E. gibboides*, *E. mutica*, and *E. recurva* were collected such that these populations also ranked among 75% of the euphausiids collected. To the north, *T. longipes* and *S. longicorne* were the abundant species, composing 70-80% of all euphausiids. These changes in species composition and dominance represent the

TABLE 2.—The smallest and largest densities of all euphausiid phases among the depth intervals sampled. Data from night tows unless marked with a plus (+) sign which indicates densities are from day tows.

	SOE transects									CalCOFI transect			
	Northern stations			Central stations			Southern stations						
Species	81	74	68	39	47	56	25	16	9	50.140	50.110	50.80	70.75
Euphausia pacifica	[1]27	9-540	72-10,783+	3-188	22-32,748	29,847	—	10-296	224-13,793	2-3	17-7,340	2-8,220	10-14,098
E. recurva	1	—	—	3	5+	1+	33	103	—	178-224	62	—	4+
E. gibboides	—	—	—	10	1-4+	—	198	9-207	2	2-82	6-26	2-9	4-24
E. mutica	—	—	—	—	—	—	—	7+	—	142-181	59-85	—	—
Tessarabrachion oculatus	1-3	11-31	2-34+	49	2-10	2	2+	1-11	9-54	2	2-16	5-20	2-8
Thysanopoda aequalis	—	—	—	—	—	—	4	7	—	4-44	—	—	—
T. acutifrons	—	1	—	—	—	—	1-2	1	—	2	2-2	—	—
T. egregia	—	—	—	—	—	—	4	2	1	3	2+	2	2+
Thysanoessa spinifera	—	—	14+	—	—	10	—	—	1-4	—	—	2-37	4-118
T. gregaria	25	2	—	33-34	81	29	1-173	3-71	6-142	4-646	2-481	3-223	7-768
T. longipes	8-109	27-197	4-134+	321	17-303	33	—	3	59-141	2	9-89	6-94	6-12
Nematoscelis tenella	—	—	—	—	—	—	—	3-4	—	—	—	—	—
N. difficilis	8	1-9	4-4+	9-9	2-7	3-3	—	33-43	89-109	15	8-26	8-512	12-189
Stylocheiron affine	—	—	—	—	—	—	62	1-18	—	2-151	2	6	11-18
S. longicorne	2-55	3-4	2+	34-52	2-53	11	1-295	17-73	26-229	8-130	2-900	2-248	4-68
S. maximum	1-5	2-2	1+	8	2-7	2	1-16	2-6	3-19	2-20	4-16	6-20	2-48
S. elongatum	—	—	—	1	1+	—	—	1-4	—	—	—	—	—
S. abbreviatum	—	—	—	2+	—	—	—	—	1+	—	—	—	—
Nematobrachion boopis	—	—	—	—	—	—	—	—	1+	2+	—	—	2-2+
N. flexipes	1-15	1-5	—	51	1-3	2	16	1-37	1-4	10-37	2-28	2-24	2-13
Number of depth intervals sampled	4	4	4	2	3	1	4	4	2	9	9	9	8

[1]A single density indicates a species was captured within only one depth interval.

complex interaction of: 1) the recruitment and mixing of species characteristic of the water masses that compose the California Current, 2) the daily vertical movements of euphausiids, 3) the ability of most species to avoid the sampling gear, and, to some extent, 4) their contagious dispersion. Consequently only the more obvious patterns have been noted.

The vertical distributions of adults and juveniles in the upper 500-700 m are summarized in Table 3 and compared with data from the southern part of the California Current. As previously mentioned, 7 of the 20 species collected appear to be diel migrants. Distances of 300 m or more were traversed by four species of *Euphausia*. Portions of other populations such as *Nematobrachion flexipes*, *T. longipes*, and *T. spinifera* may migrate up to 200 m.

The larval phases of most species live in the upper 150 m. *Tessarabrachion oculatus* and *Stylocheiron* spp. larvae were found more often below the thermocline. The young of *Euphausia* spp. tended to occupy and migrate through the same depths as the older stages. In nearly all instances, differences in density between day and night catches of larvae were small.

The nonmigrating species included *Thysanoessa gregaria*, *Tessarabrachion oculatus*, *S. maximum*, *S. affine*, and *S. longicorne*. The first three species were usually scattered throughout a broad vertical range. The other two species, *S. affine* and *S. longicorne*, were vertically segregated and occurred within much narrower depth intervals. The different strata occupied by these two nonmigrating species was also observed in other regions by Brinton (1967), Baker (1970), and Youngbluth (1975).

DISCUSSION

Differences in the distribution patterns of many species of zooplankton have been associated with their response to environmental gradients, particularly temperature and illumination (Harris 1953; Lewis 1954; Banse 1964; Boden and Kampa 1967). In this study, the causative factors influencing vertical and horizontal distributions are difficult to elucidate. It is clear, however, that the thermocline was an upper distribution boundary for several species, e.g., *T. oculatus*, *E. gibboides*, *S. affine*, *S. longicorne*, and *S. maximum*. In the southern part of the California Current, the upper range of these species was also restricted by the thermocline (Brinton 1967). Studies on the tolerance of *E. pacifica* to changes in temperature and salinity suggest that other unknown factors probably regulate its distribution in the California Current (Gilfillan 1972a, b).

Recently Isaacs et al. (1974) have proposed that "by responding to light intensity, most vertically migrating marine creatures are directed to food. ... In areas of low standing crops of phytoplank-

TABLE 3.—Comparisons of diel changes in the vertical distributions of adult and juvenile euphausiids. Depth ranges (m) are 10% and 90% levels.

Species	Central California Current		Southern California Current (Brinton 1967)	
	Day	Night	Day	Night
Euphausia pacifica	20-500	0-450	150-425	0-150
E. recurva	300-600	0-50	180-550	0-150
E. gibboides	300-600	10-150	[1]300-500	40-120
E. mutica	[2]370-470	0-150	—	—
Tessarabrachion oculatus	70-450	70-450	—	—
Thysanoessa spinifera	125-300	0-150	—	—
T. gregaria	0-200	0-350	20-180	0-250
T. longipes	0-800	0-800	—	—
Nematoscelis difficilis	0-400	0-400	[3]50-200	0-275
Stylicheiron affine	40-100	35-100	[3]50-200	15-250
S. longicorne	100-350	100-350	125-300	125-300
S. maximum	70-450	70-450	[4]130-200	[4]130-200
Nematobrachion flexipes	200-500	0-130	100-450	100-350
Sampling range (m)	0-800		0-600	
Sampling interval	50-150		25-100	
Gear employed	Bongo nets		Leavitt nets	
Mesh opening	0.333 mm		0.550 mm	

[1]Adults only.
[2]Based on seven specimens from one station.
[3]Mostly juveniles.
[4]Maximum concentration of juveniles.

ton, daylight penetrates further into the ocean causing the migrating animals to descend deeper. In the turbid water associated with high standing crop, the migrating forms remain closer to the surface." Observations on the vertical distribution and daily movements of one euphausiid species in this study lend support to this hypothesis. In more turbid, upwelled water near the coast where standing stocks of phytoplankton were greater (e.g., CalCOFI 50.80), populations of juvenile *E. pacifica* were larger and extended over wider vertical ranges but their diel vertical migrations were not pronounced. In clearer, more oligotrophic waters farther offshore (e.g., CalCOFI 50.110; SOE 16, 47, 74), populations were reduced in size, occupied deeper, usually narrower depth intervals, and daily vertical movements were more obvious. From these few observations it appears that density levels and migration intensities of this species may be coupled with the standing stock of phytoplankton in surface waters.

The persistence of nonmigrating forms, e.g., *Stylocheiron* spp., within the same, relatively narrow depths day and night in waters of varying origin and the recurrence of the finding in this and other studies (Brinton 1967; Youngbluth 1975) that only a portion of a population categorized as a migrating form, e.g., *Euphausia* spp., may actually make daily vertical movements to surface waters, suggest that factors in addition to temperature and light act to regulate the distributions recorded. These observations indicate that more attention should be directed toward sampling those horizons where zooplankton populations are concentrated to determine how distributional and behavioral patterns are structured by the physical and biological fluctuations within their preferred habitats.

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LITERATURE CITED

ALTON, M. S., AND C. J. BLACKBURN.
1972. Diel changes in the vertical distribution of the euphausiids, *Thysanoessa spinifera* Holmes and *Euphausia pacifica* Hansen in coastal waters of Washington. Calif. Fish Game 58:179-190.

ALVARIÑO, A.
1965. Distributional atlas of Chaetognatha in the California Current region. Calif. Coop. Oceanic Fish. Invest., Atlas 3, 291 p.

BAKER, A. DE C.
1970. The vertical distribution of euphausiids near Fuerteventura, Canary Islands ('Discovery' SOND Cruise, 1965). J. Mar. Biol. Assoc. U.K. 50:301-342.

BANSE, K.
1964. On the vertical distribution of zooplankton in the sea. Prog. Oceanogr. 2:53-125.

BARHAM, E. G.
1957. The ecology of sonic scattering layers in the Monterey Bay area. Stanford Univ., Hopkins Mar. Stn. Tech. Rep. 1, 182 p.

BERNER, L. D., JR.
1957. Studies on the Thaliacea of the temperate northeast Pacific Ocean. Ph.D Thesis, Scripps Inst. Oceanogr., Univ. Calif., San Diego, 144 p.
1967. Distributional atlas of Thaliacea in the California Current region. Calif. Coop. Oceanic Fish. Invest., Atlas 8, 322 p.

BIERI, R.
1959. The distribution of the planktonic Chaetognatha in the Pacific and their relationship to the water masses. Limnol. Oceanogr. 4:1-28.

BODEN, B. P., M. W. JOHNSON, AND E. BRINTON.
1955. The Euphausiacea (Crustacea) of the North Pacific. Bull. Scripps Inst. Oceanogr., Univ. Calif. 6:287-400.

BODEN, B. P. AND E. M. KAMPA.
1967. The influence of natural light on the vertical migrations of an animal community in the sea. Symp. Zool. Soc. Lond. 19:15-26.

BOLIN, R. L. AND D. P. ABBOTT.
1963. Studies on the marine climate and phytoplankton of the central coastal area of California, 1954-1960. Calif. Coop. Oceanic Fish. Invest., Rep. 9:23-45.

BRINTON, E.
1960. Changes in the distribution of euphausiid crustaceans in the region of the California Current. Calif. Coop. Oceanic Fish. Invest., Rep. 7:137-146.
1962a. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr., Univ. Calif. 8:51-269.
1962b. Variable factors affecting the apparent range and estimated concentration of euphausiids in the North Pacific. Pac. Sci. 16:374-408.
1967. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12:451-483.

CUSHING, D. H.
1971. Upwelling and the production of fish. Adv. Mar. Biol. 9:255-334.

DAY, D. S.
1971. Macrozooplankton and small nekton in the coastal waters off Vancouver Island (Canada) and Washington,

spring and fall of 1963. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Spec. Sci. Rep. Fish. 619, 94 p.

DODIMEAD, A. J., F. FAVORITE, AND T. HIRANO.
1963. Salmon of the North Pacific Ocean. Part II. Review of the oceanography of the subarctic Pacific region. Int. North Pac. Fish. Comm. Bull. 13, 195 p.

FLEMINGER, A.
1964. Distributional atlas of calanoid copepods in the California Current region, part I. Calif. Coop. Oceanic Fish. Invest., Atlas 2, 313 p.
1967. Distributional atlas of calanoid copepods in the California Current region, part II. Calif. Coop. Oceanic Fish. Invest., Atlas 7, 213 p.

FROLANDER, H. F.
1962. Quantitative estimations of temporal variations of zooplankton off the coast of Washington and British Columbia. J. Fish. Res. Board Can. 19:657-675.

GILFILLAN, E.
1972a. Seasonal and latitudinal effects on the responses of *Euphausia pacifica* Hansen (Crustacea) to experimental changes of temperature and salinity. *In* A. Y. Takenouti (editor), Biological oceanography of the northern North Pacific Ocean, p. 443-463. Idemitsu Shoten, Tokyo, Jap.
1972b. Reactions of *Euphausia pacifica* Hansen (Crustacea) from oceanic, mixed oceanic-coastal and coastal waters of British Columbia to experimental changes in temperature and salinity. J. Exp. Mar. Biol. Ecol. 10:29-40.

HARRIS, J. E.
1953. Physical factors involved in vertical migration of plankton. Q. J. Microsc. Sci. 94:537-550.

HEBARD, J. F.
1966. Distribution of Euphausiacea and Copepoda off Oregon in relation to oceanographic conditions. Ph.D. Thesis, Oregon State Univ., Corvallis, 94 p.

ISAACS, J. D., A. FLEMINGER, AND J. K. MILLER.
1969. Distributional atlas of zooplankton biomass in the California Current region: Spring and fall 1955-1959. Calif. Coop. Oceanic Fish. Invest., Atlas 10, 252 p.

ISSACS, J. D., S. A. TONT, AND G. L. WICK.
1974. Deep Scattering Layers: vertical migration as a tactic for finding food. Deep-Sea Res. 21:651-656.

JOHNSON, M. W., AND E. BRINTON.
1963. Biological species, water-masses and currents. *In* M. N. Hill (editor), The Sea, Vol. 2, p. 381-414. Interscience, N.Y.

KIN'DYUSHOV, V. I.
1970. Seasonal changes of water masses in the California region of the Pacific Ocean. [In Russ., Eng. summ.] Okeanologia. 10:596-606.

LAURS, R. M.
1967. Coastal upwelling and the ecology of lower trophic levels. Ph.D. Thesis, Oregon State Univ., Corvallis, 121 p.

LEWIS, J. B.
1954. The occurrence and vertical distribution of the Euphausiacea of the Florida Current. Bull. Mar. Sci. Gulf Caribb. 4:265-301.

LONGHURST, A. R.
1967. Diversity and trophic structure of zooplankton communities in the California Current. Deep-Sea Res. 14:393-408.

MCGOWAN, J. A.
1967. Distributional atlas of pelagic molluscs in the California Current region. Calif. Coop. Oceanic Fish. Invest., Atlas 6, 218 p.
1971. Oceanic biogeography of the Pacific. *In* B. M. Funnell and W. R. Riedel (editors), The micropaleontology of oceans, p. 3-74. Camb. Univ. Press., Lond.

MCGOWAN, J. A. AND D. M. BROWN.
1966. A new opening-closing paired zooplankton net. Scripps Inst. Oceanogr. Ref. 66-23, 56 p.

MALONE, T. C.
1971. The relative importance of nannoplankton and netplankton as primary producers in the California Current system. Fish. Bull., U.S. 69:799-820.

OKUTANI, T. AND J. A. MCGOWAN.
1969. Systematics, distribution, and abundance of the epiplanktonic squid (Cephalopoda, Decapoda) larvae of the California Current, April, 1954–March, 1957. Bull. Scripps Inst. Oceanogr., Univ. Calif. 14, 90 p.

PIEPER, R. E.
1967. Mesopelagic faunal discontinuities in the eastern North Pacific. AC Electronic-Def. Res. Lab. Rep. TR67-19, 38 p.

PONOMAREVA, L. A.
1963. Euphausiids of the North Pacific, their distribution and ecology. Akad. Nauk SSSR Inst. Okeanol. (Translated by Israel Program Sci. Transl., Jerusalem 1966, IPST cat. no. 1368, 154 p.)

REGAN, L.
1968. *Euphausia pacifica* and other euphausiids in the coastal waters of British Columbia: Relationships to temperature, salinity and other properties in the field and laboratory. Ph.D. Thesis, Univ. British Columbia, Vancouver, 235 p.

REID, J. L., JR., G. L. RODEN, AND J. G. WYLLIE.
1958. Studies of the California Current system. Calif. Coop. Oceanic Fish. Invest., Prog. Rep., 1 July to 1 Jan. 1958, p. 27-57.

THRAILKILL, J. R.
1963. Zooplankton volumes off the Pacific Coast, 1959. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 414, 77 p.

WHITTAKER, R. H.
1952. A study of summer foliage insect communities in the Great Smokey mountains. Ecol. Monogr. 22:1-44.

YOSHIDA, K.
1955. Coastal upwelling off the California coast. Rec. Oceanogr. Works Jap., New Ser. 2(2):8-20.

YOUNGBLUTH, M. J.
1973. The vertical distribution, diel migration, and community structure of euphausiids. Ph.D. Thesis, Stanford Univ., Palo Alto, Calif., 298 p.
1975. The vertical distribution and diel migrations of euphausiids in the central waters of the eastern South Pacific. Deep-Sea Res. 22:519-536.

THE APPLICATION OF SYSTEMATIC SAMPLING TO A STUDY OF INFAUNA VARIATION IN A SOFT SUBSTRATE ENVIRONMENT[1]

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ABSTRACT

Stratified systematic sampling was applied to an intertidal macrofauna sediment study. A stratified systematic sampling plan retains the advantages of the more common fixed level transect sample, and possesses additional advantages which recommend it for use in some intertidal studies. The field data collected in this study demonstrated the effectiveness of stratified systematic sampling for quantifying both sediment and population characteristics along a sediment gradient, and for the testing of biological hypotheses.

Intraarea, interarea, and interseason hypotheses about sediment composition were tested in terms of particle size distributions. Populations of bivalves and polychaetes were simultaneously sampled and hypotheses concerning spatial and seasonal variations in an intertidal mud flat were tested. Experimental results using stratified systematic sampling suggest that Newell's hypothesis can be extended to encompass temporal variation. Fine sediment grades (silty areas) may act to insulate infauna against the extremes of seasonal stresses.

Sediment composition, as measured by the average percentage composition by weight of various grain sizes, was not sufficient to predict macrofaunal presence.

The study of the complex relationship existing between macrofauna (e.g., bivalves and polychaetes) and their soft substrate environment is of wide interest in marine biology. Soft sediments are both a shelter from predators and a food source for deposit feeders. The particle size distribution of the sediment influences such factors as food availability, the depth of the aerobic layer, water content, pH differentials, and growth rates. Detrital content and particle size distribution of the sediment are largely determined by the hydrodynamics of currents. However, Rhoads (1967) demonstrated that macrofauna modify sediment stability, composition, and water content by activities such as building tubes, ingesting sediment and detritus (to remove bacteria from sediment particles), depositing feces, etc. The particle size distribution of the sediment is, therefore, one measure of certain types of biological activity (Newell 1965).

Studies in soft substrate environments usually involve sediment samples which contain large numbers of macrofaunal species in different densities as well as different particle size distributions. Then, it may be necessary to make comparisons between samples which may call for the use of statistical methods as found in standard textbooks (e.g., Sokal and Rolf 1969). The validity of tests of comparisons, however, must rest upon the application of valid sampling plans in the field, but most valid sampling plans do not meet the needs of the ecologist. This paper reports on the use of stratified systematic sampling which, to our knowledge, is heretofore unused in the marine literature. Stratified systematic sampling seems to meet the needs of most studies that would have used transecting methods which, generally, are statistically unacceptable. The sampling method is applied to a study of animal and sediment gradients in a basically marine embayment subject to seasonal variation in density of animals and algae. Hypotheses comparing areas of different sediment composition in the winter, spring, and summer are tested using animal-presence and sediment-particle-size data collected using a stratified systematic sampling plan. The bay is shown to contain a sediment gradient from fine silt to coarse sand, with an associated polychaete distribution expressed by both the number of animals per species and by the number of species found.

A variety of sampling methods are described in the literature. For example, the works of Skellam (1958) and Sen et al. (1974) presented different

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types of transect methods, and Saila and Gaucher (1966), Russell (1972), and Loesch (1974) described subtidal stratified random sampling methods.

Transecting methods used in the soft substrate of the intertidal zone usually involve the choice of a narrow belt of one or two sampling units in width, placed perpendicular to the water line. Samples are collected at fixed and predetermined tidal levels (e.g., every 10 m) to correspond to changes in such things as algal and sediment composition (Matthiessen 1960; Vassallo 1969; Warme 1971; Bloom et al. 1972). This method will be referred to as fixed level transect sampling (FLTS). A common denominator in this type of work is that no probability model is used in selecting the location of the sampling units. An alternative to FLTS is simple or stratified random sampling where the discrete uniform probability distribution underlies the selection of sample sites. The disadvantage of random sampling is that there is no guarantee that sample sites will be in those areas where experimental interest is focused. However, without an underlying probability model, valid statistics may not be estimated (Cochran 1963) because the sample sites may not be independently located and subsequent statistical tests may be invalid. These points are often overlooked.

Stratified systematic sampling (SSS) is proposed as an alternative to the FLTS method currently popular in intertidal fieldwork. The usefulness of SSS is demonstrated by applying it to a study of spatial and temporal variation in a macrofauna-sediment relationship. This field study was conducted at Garrison Bay (Figure 1), a small embayment on San Juan Island, Wash. (lat. 48°35′N, long. 128°08′W).

MATERIALS AND METHODS

Applications of systematic sampling are found in the forestry literature (Osborne 1942; Finney 1948; Matern 1960; Faber 1972). Mathematical details are found in sampling texts such as Cochran (1963), Raj (1968), or Sukhatme and Sukhatme (1970) and in many theoretical papers.[4] Systematic sampling assumes that the sampling units in the area to be studied are numbered consecutively. The attractiveness of the method is increased by the relatively sessile nature of many intertidal

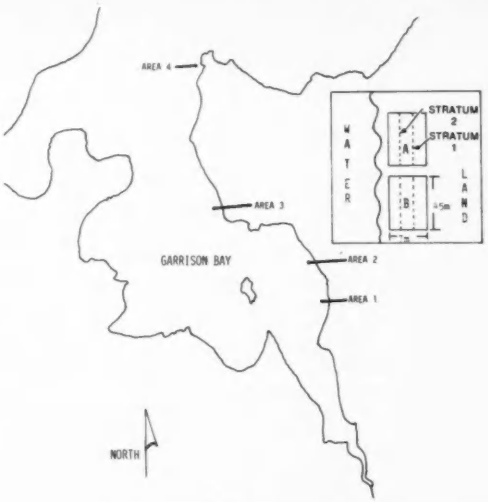

FIGURE 1.—Shoreline of Garrison Bay showing the location of the four study areas. Insert shows the representative arrangement of the subareas (A and B) and the strata (1 and 2) in these areas.

organisms. From N sampling units numbered 1, 2, . . ., N; n sampling units are selected, all evenly spaced at a distance of K sampling units apart. Thus, $N = nK$. The location of the first unit to actually be sampled is randomly chosen by selecting a number between 1 and K from a table of random numbers. Hence, systematic sampling is based upon a uniform probability distribution (Raj 1968). SSS is a variation in which the region is divided into strata, e.g., at the locations of the fixed levels where samples would have been collected using FLTS. Each stratum is independently sampled in the manner described above.

Four regions with different sediment compositions were a priori defined in the intertidal area of Garrison Bay (Figure 1). Representative areas within these regions were sampled in the winter (January and February), spring (May and June), and summer (July and August) 1974. A north-south sediment gradient exists because fine sediment is deposited at the closed end of the bay where the water is less turbulent. Thus, the south (closed) end of the bay consists principally of fine grades of sediment, while the north (open) end consists mainly of coarser grades. Visual examination indicates that perpendicular to the water, there is a sediment gradient as well as a zonation of intertidal animals. However, the statistical comparisons of the data from strata, which were

[4]Scherba, S., Jr., and V. F. Gallucci. 1976. Quantification of species-presence gradients by stratified systematic sampling and the autocovariance function. Unpubl. manuscr., 15 p.

placed parallel to the water, do not show the gradient. This is probably a consequence of the short distance between strata.

Field Procedures

Within each region (Figure 1), a rectangular study area was defined, measuring 95 m in length parallel to the waterline, and approximately 7 m wide, perpendicular to the waterline. Two parallel strata, approximately 2.5 m apart, were placed within each area, parallel to the waterline. The stratum at the highest tidal level was designated stratum 1 while the lower stratum was designated stratum 2. Stratum 1 within the areas was located at -1.4, -1.2, -1.1, and -1.2 feet in areas 1, 2, 3, and 4 respectively; while stratum 2 in those same areas was at -1.5, -1.7, -1.5, and -1.6 feet.[5] The study areas were numbered one (1) to four (4) (south to north) and defined by stakes marked with fluorescent tape for night identification.

It is necessary to test the homogeneity of sediment composition within a region if the areas are to be considered representative. This test was accomplished by dividing each area into two subareas,[6] separated by 5 m, and denoted as A (for the northmost subarea) and B (for the southmost). Each subarea contained about 448 sampling units. Two samples were then collected on each stratum, from each subarea, using a systematic sampling plan.

Each subarea was considered to contain separate populations, and the two population Kolmogorov-Smirnov procedure with $n = 4$ (Conover 1971) was applied to the data collected. This use of both subareas was carried out only for the winter sampling. Winter sampling of the subareas was done on: 8 January 1974 (1A, 1B), 9 January 1974 (3A, 3B), 2 February 1975 (2A, 2B), and 3 February 1974 (4A, 4B).

Spring and summer sampling was conducted only in subareas 1B, 2A, 3A, and 4A as follows: 24 May 1974 (1B, 3A), 21 June 1974 (2A, 4A), 19 July 1974 (1B, 4A), and 16 August 1974 (2A, 3A). Each stratum in these four subareas was independently sampled during these two seasons with $n = 4$ on each stratum.

All samples were collected using a thick-walled, cylindrical corer made of polyvinyl chloride pipe, 10 cm inside diameter and 18 cm long. The corer was pressed into the sediment to 18 cm, and its contents removed by hand, placed in a labeled plastic bag, and taken to the laboratory. Each sample was passed through a 1-mm sieve, and the contents retained by the sieve were sorted twice by eye to remove all bivalves and polychaetes (the only members of the macrofauna identified). These organisms were placed in 80% ethanol and 8% formaldehyde, respectively, for later identification. Only the common bivalves and polychaetes were identified to genus and species. The sediment portion of each sample was dried at 100°C for approximately 4 h. The method used to quantify the particulate properties of the sediment was the percentage composition by weight of selected sediment grain sizes. A mechanical shaker was used to pass the sediment portion of each sample through a series of Wentworth sieves (1.981, 0.495, 0.246, 0.124, 0.063 mm). The contents of each sieve were weighed and recorded as percentage of the total weight of that sample.

Statistical Procedures

Estimates of the variances of the sample means, obtained from SSS were approximated by the estimate of the variance of the sample mean from a simple random sample (see Cochran 1963), i.e., by using

$$\text{var}(\bar{y}) = \left(\frac{N-n}{N}\right)\left(\sum_{j=1}^{n}(y_j - \bar{y})^2\right)/n(n-1)\Big)$$

where $\bar{y} = \left(\sum_{j=1}^{n} y_j\right)/n.$

The rational for this approximation is discussed later.

Two statistical tests were used to quantify the sampling results. The K sample Kolmogorov-Smirnov (K-S) test with $\alpha = 0.10$, using the T_3 test statistic (Birnbaum and Hall 1960; Conover 1971), was used to test hypotheses about variation in sediment composition. The chi-square test for several multinomials with $\alpha = 0.05$ (Conover 1971) was used to test hypotheses about variation in bivalve and polychaete community structure.

In the within-area sediment homogeneity test empirical distribution functions were constructed for each subarea. The K-S test ($\alpha = 0.10$) was then used to test the null hypothesis (H_0) of equality of

[5]Tidal heights are reported in feet to conform with U.S. Coast and Geodetic Survey Tide Tables.

[6]We thank A. R. Sen for this suggestion.

these distribution functions. Using winter samples only, the test failed to reject H_0; thus, the data from each A and B subarea pair were combined and considered to be one subarea for comparison to the subareas sampled in the spring and summer. Hence, all data were analyzed as if they had been collected from four equal sized subareas, of dimensions 45 m by 7 m, during each season, using a sample of size four on each stratum.

The empirical cumulative distribution functions were constructed from the data by defining a random variable X as the sum of the percent of the total sediment weights retained in the sieve sizes <0.063, 0.063, and 0.124 mm. The random variable X takes a value of each sample, in each subarea, on each stratum. Thus, the empirical distribution functions constructed from this data characterized the sum of the weights of three finest sediment grades (and by subtraction from 100%, the three coarsest grades as well) for each stratum in each subarea. These three sieve sizes were grouped together because they constitute what may be called the finer grades of sediment and they probably have the greatest biological impact (Newell 1965). If the grain size which is of principal importance to the organisms is known, then the random variable could be chosen accordingly. There is much evidence that grain size is important to the organisms (e.g., see Loosanoff and Tommers 1948; Sanders 1958; Wieser 1959; Gray 1974). Subject to this limitation of comparing only the finer sediment groups, the sediment data may be statistically compared stratum to stratum in any one subarea, between subareas, or in combinations of these, both within or between seasons.

In each case, the null hypothesis for the K-S test on sediment was

$$H_0: F_1(x) = F_2(x) = \ldots = F_k(x) \qquad (1)$$

and the alternative

H_a: there is at least one inequality where $F_j(x)$ is the cumulative distribution function of the random variable X corresponding to area j.

The statistical analysis of the distribution of animal populations was based upon standard chi-square procedures (Conover 1971). Let the random variable Z have a multinomial distribution where the number of classes corresponds to the number of species types used, and the number of trials is the total number of individuals of all species. The chi-square test was applied to those species types with entries in the expected value table which were either greater than unity, or at least, not far below unity. All species identified are listed, but, in certain cases, some species were grouped into families for the analysis; these are noted in the tables of data. Grouping of data is often advisable on statistical or biological grounds depending upon the objectives of the study. When data were grouped in this study, the grouping was dictated by sample sizes and was consistent with biological facts such as where the organisms occur in Garrison Bay, their modes of feeding, and their taxonomy.

The data were organized into contingency tables for a multinomial distribution. We denote the probability of a randomly selected value from the ith population as being classified in the jth class by P_{ij}. The columns of the table represent species (classes) while the rows represent populations, i.e., a particular stratum in a given subarea during a specific season. The null hypothesis may be stated as:

$$H_0: P_{1j} = P_{2j} = \ldots = P_{rj} \text{ for all } j; j = 1, 2, \ldots, c, \qquad (2)$$

and the alternative

H_a: there is at least one $P_{ij} \neq P_{kj}$ for some j and pair i, k where r equals the number of rows and c equals the number of columns. Under H_0,

$$P_{11} = P_{21} = \ldots = P_{r1} = P_1$$
$$\vdots$$
$$P_{1c} = P_{2c} = \ldots = P_{rc} = P_c$$

where $\hat{P}_j = C_j/N$; C_j = sum of observations in column j; N = total number of observations from all samples; and $\hat{P}_j$ estimates P_j. When a row or column of a particular contingency table equalled zero, it was not possible to reach a decision about the chi-square null hypothesis. To maintain consistent comparisons, no alteration of the contingency tables was made in such cases. The results of some of these tests of homogeneity are summarized in the next section.

RESULTS

The sampling data and the estimates of the variances of the sample means appear in Tables

1-3. It was necessary to pool the winter samples that were used to test for homogeneity (see Statistical Procedures) within each area. The samples in each area were considered to be from one subarea to correspond to the subareas used for the spring and summer sampling. The spring and summer samples were collected exclusively from subareas 1B, 2A, 3A, and 4A. The data in Tables 2 and 3 are for the species of bivalves and polychaetes which could be identified from the samples.

Sediment

The sediment data (Table 1) and statistical analyses confirm the existence of a particle size gradient from the closed (south) end to the open (north) end of the bay. Subareas 1B and 4A appear similar in Table 1, but subarea 1B is located in the closed end of Garrison Bay (Figure 1) which is much muddier with more fine grained particles and has poorer drainage than subarea 4A. Because the data suggest that subareas 1B and 4A contain approximately the same proportion of coarse grain particles (i.e., ≥1.981 mm), a qualitative description was used to supplement the quantitative analysis based on grain size composition by percentage weight: the 1.981-mm sieve in samples from subarea 1B contained large amounts of shell fragments, which will remain in suspension longer due to their flattened shape, while the same sieve size in subarea 4A contained mostly round pebbles, which settle more rapidly, and few shell fragments. Thus, despite their heavy weight, shell fragments were carried into the quiet part of the bay.

Samples from subarea 2A often had added weight in the 1.981-mm sieve in the form of rocks of about 5 cm across. This is probably the result of the activities of early settlers or of recent anthropoligical investigations.

The K-S procedures ($\alpha = 0.10$) confirmed the existence of a north-south sediment gradient between similarly numbered strata in all seasons between all four subareas. All six of the null hypotheses (1) of equality were rejected.

The sources of this gradient were located by using the K-S procedure ($\alpha = 0.10$) to compare all combinations of subarea pairs and seasons for similarly numbered strata. This resulted in the testing of 36 null hypotheses (1) of no difference, of which 25 were rejected and the remainder accepted. Thus, a gradient may be said to be the result of

TABLE 1.—Average percent of total weight of sediment in each of six particle size categories: W = Winter, Sp = Spring, Su = Summer. The numbers in parentheses are estimates of the variance of sample means.

Particle size (mm)	Subarea 1B						Subarea 2A					
	Stratum 1			Stratum 2			Stratum 1			Stratum 2		
	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
<0.063	6.7(1.0)	10.7(0.28)	6.7(1.0)	4.3(0.64)	9.5(4.9)	6.9(0.31)	10.4(2.6)	6.8(0.99)	7.9(1.5)	9.2(4.2)	5.0(0.04)	5.4(0.22)
0.063	8.5(0.77)	11.2(1.3)	9.4(0.74)	5.6(1.4)	9.1(1.3)	9.4(0.43)	7.9(3.5)	7.1(1.2)	8.2(1.5)	8.0(1.7)	4.6(0.11)	5.9(0.10)
0.124	13.7(1.3)	20.9(7.8)	15.6(1.5)	11.9(6.0)	19.4(5.2)	16.7(2.7)	10.3(10)	11.3(0.71)	11.8(1.8)	10.6(1.9)	7.5(0.05)	11.2(0.02)
0.246	11.7(0.04)	15.5(4.8)	15.5(5.3)	10.9(3.0)	15.9(0.94)	16.5(6.5)	9.1(3.3)	11.5(0.33)	10.5(0.57)	9.2(0.35)	9.0(0.93)	12.4(0.15)
0.495	16.2(1.0)	15.3(3.4)	18.5(0.58)	15.0(2.7)	15.1(1.7)	16.9(4.2)	13.2(1.4)	14.8(1.2)	13.2(3.1)	12.7(0.80)	11.7(0.51)	13.3(0.20)
1.981	43.2(6.0)	26.2(21)	34.3(6.4)	52.3(59)	30.9(36)	33.5(48)	49.0(72)	48.8(11)	48.4(26)	50.2(20)	62.2(4.2)	51.8(2.1)

Particle size (mm)	Subarea 3A						Subarea 4A					
	Stratum 1			Stratum 2			Stratum 1			Stratum 2		
	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
<0.063	6.0(2.1)	10.9(1.5)	7.1(1.8)	8.0(3.2)	11.9(0.11)	9.2(1.2)	3.4(0.07)	4.6(0.39)	4.5(0.19)	3.0(0.11)	3.8(0.26)	4.8(0.49)
0.063	14.6(7.4)	20.8(5.7)	16.9(4.6)	17.9(6.3)	22.0(2.6)	17.8(1.9)	9.9(0.80)	9.5(1.2)	9.2(1.6)	7.7(0.38)	9.8(1.4)	8.3(0.34)
0.124	37.0(29)	38.1(8.0)	35.9(32)	39.2(7.3)	26.0(1.1)	30.6(1.7)	16.2(2.8)	20.2(4.6)	19.6(17)	9.1(0.19)	22.3(12)	22.6(4.6)
0.246	12.5(1.7)	8.4(0.52)	11.8(9.1)	14.5(11)	10.6(0.13)	11.9(2.2)	3.4(0.27)	9.1(0.95)	6.6(0.83)	4.4(0.45)	10.4(5.5)	10.6(4.6)
0.495	13.2(12)	7.7(0.55)	12.6(5.8)	10.5(3.1)	12.5(0.11)	12.5(1.9)	15.0(2.3)	14.9(0.25)	15.3(0.58)	14.6(0.72)	19.3(0.85)	20.2(0.81)
1.981	16.7(33)	16.0(15)	15.6(37)	10.4(17)	16.9(5.5)	17.9(5.6)	52.2(6.8)	41.2(16)	44.8(37)	61.1(4.6)	34.6(39)	30.4(31)

different subareas being dissimilar in a season. In particular, it was found that: 1) in the spring, subareas 1B and 2A were significantly different on both strata, while only stratum 2 in those subareas was significantly different in the summer; 2) both strata in subareas 1B and 3A and subareas 3A and 4A were significantly different throughout all seasons; and 3) stratum 1 of subareas 2A and 4A were significantly different only in the spring, while stratum 2 in these subareas was different in each season.

The K-S procedure ($\alpha = 0.10$) was used to test sediment composition homogeneity both between the strata of a given subarea and among the three seasons for a single stratum. Over half of these null hypotheses were accepted. Therefore, sediment composition of the strata remained largely stable throughout the three seasons and apparently lacked a consistent zonation perpendicular to the water.

Polychaetes

Table 2 shows that the dominant polychaete species vary according to season and sediment type. These species were found to be: *Lumbrineris bicirrata*, *Dorvillea japonica*, *Scoloplos pugettensis*, *Cirratulus cirratus*, and *Capitella capitata*. In this study the dominant species is the species with the largest number of individuals.

Spatial and temporal dominance patterns may be seen. In subarea 2A, the dominant organism is generally *D. japonica* (in all seasons on stratum 2 and in the winter and spring on stratum 1). *Capitella capitata* is usually the dominant species in subarea 3A (*S. pugettensis* being dominant there only in the winter on stratum 1). The increase in this species during the summer, as compared to the spring, on both strata of subarea 3A may have been influenced by the presence of a dense algal mat of *Enteromorpha* sp. which covered large intertidal areas. Subarea 4A has the greatest fluctuation with respect to the dominant species. On stratum 2 of subarea 4A, *C. capitata* is dominant in the spring and summer, replacing *L. bicirrata*, the winter dominant. *Capitella capitata* is dominant only in the spring on stratum 1 of subarea 4A; *C. cirratus* is dominant in both winter and summer. Subarea 1B shows the smallest seasonal fluctuation of any subarea in both total polychaete assemblage and dominant species. *Cirratulus cirratus* is dominant on both strata in the spring and summer, replacing the winter dominants *S. pugettensis* (on stratum 1) and *L. bicirrata* (on stratum 2).

No simple seasonal pattern is discernible on the strata of the various subareas (see Table 2). Stratum 1 in both subareas 1B and 3A shows a steady increase in total number of individuals between spring and summer. In the cases of subarea 1B (stratum 2), subarea 2A (strata 1 and 2), and subarea 4A (stratum 2), the largest number of individuals is present in the spring. Subarea 3A (stratum 2) and subarea 4A (stratum 1) have the largest number of individuals in the winter, due to *Cirratulus capitata* and *Capitella cirratus*, respectively. However, there is insufficient data to conclude that stratum 2 is uniformly sustaining the greatest total numbers of individuals seasonally (perhaps due to the small horizontal distance separating the strata in each subarea).

Table 2 shows that it is possible to rank the subareas, in descending order, with regard to number of species present: subareas 1B, 4A, 2A, and 3A; as well as with respect to the total number of individuals: subareas 1B, 2A, 4A, and 3A. There are occasional seasonal reordering of these ranks.

Statistical analysis using the chi-square procedures ($\alpha = 0.05$, 33 df) confirmed the existence of a within season polychaete distribution (for the 12 groups used in the analysis) on identically numbered strata, between the four subareas in five of these six comparisons. The one exception was the comparison of stratum 1, between the four subareas, during the winter. In that instance, a "no decision" result was reached.

To investigate the sources of this difference in distribution, the polychaete assemblage on similarly numbered strata, all combinations of subarea pairs and season were examined using chi-square tests ($\alpha = 0.05$, 11 df). Eleven of these 36 null hypotheses (2) resulted in a "no decision" conclusion while the remaining 25 were rejected using this analysis. In the case of stratum 2, the null hypotheses comparing subareas 1B and 2A, 1B and 3A, 1B and 4A, 3A and 4A, and 2A and 4A were rejected in all seasons. The fluctuation of this biotic distribution in time (season) and space (sample area) is apparent.

The homogeneity (2) of the polychaete assemblage between the three seasons for a single stratum was examined using chi-square tests ($\alpha = 0.05$, 22 df). Of the eight null hypotheses of homogeneity (2), six were rejected (i.e., both strata 1 and 2 in both subareas 1B and 3A, and stratum 2 in both subareas 2A and 4A). The two remaining

TABLE 2.—Total number of individuals of the eighteen common polychaete species in four samples: W = Winter, Sp = Spring, Su = Summer. The numbers in parentheses are estimates of the variance of sample means.

	Subarea 1B						Subarea 2A					
	Stratum 1			Stratum 2			Stratum 1			Stratum 2		
Species - Number	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
Harmothoe multisetosa - 1	2(0.08)	1(0.06)	0(0)	1(0.06)	1(0.06)	0(0)	1(0.06)	4(0.49)	4(0.17)	1(0.06)	3(0.06)	1(0.06)
Eulalia parvoseta - 2	0(0)	2(0.25)	0(0)	0(0)	4(0.49)	0(0)	0(0)	0(0)	0(0)	0(0)	1(0.06)	0(0)
Gyptis brevipalpa[1] - 3	1(0.06)	4(0.49)	10(2.7)	2(0.08)	3(0.06)	3(0.23)	0(0)	0(0)	0(0)	1(0.06)	4(0.17)	2(0.08)
Ophiodromus pugettensis[1] - 4	1(0.06)	6(2.2)	10(2.4)	0(0)	7(0.39)	5(0.89)	0(0)	0(0)	1(0.06)	0(0)	4(0.99)	9(2.0)
Platynereis bicanaliculata - 5	2(0.08)	2(0.25)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)
Nephtys caeca - 6	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Glycera capitata[2] - 7	4(0.17)	3(0.56)	3(0.23)	1(0.06)	2(0.08)	1(0.06)	4(0.50)	1(0.06)	2(0.08)	0(0)	1(0.06)	0(0)
Diopatra ornata - 8	0(0)	0(0)	0(0)	0(0)	2(0.08)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)	0(0)
Lumbrineris bicirrata[2] - 9	8(3.9)	31(4.9)	64(26.6)	36(3.7)	75(4.5)	72(5.1)	39(3.4)	55(39)	22(3.5)	20(1.5)	64(21)	45(18)
Dorvillea japonica[2] - 10	10(1.7)	50(22)	81(6.2)	15(1.1)	85(30)	36(13.7)	78(49)	96(36)	48(26)	35(11.6)	165(119)	56(61)
Scoloplos pugettensis[2] - 11	27(1.5)	26(8.8)	42(12.3)	6(1.4)	8(0.99)	4(0.49)	15(3.2)	43(25)	52(27)	9(1.1)	20(4.1)	1(0.06)
Naineris quadricuspida[2] - 12	0(0)	2(0.25)	7(2.0)	0(0)	5(0.06)	2(0.08)	25(9.3)	12(0.83)	14(1.4)	6(0.41)	39(38)	5(0.39)
Cirratulus cirratus[2] - 13	7(0.39)	124(183)	127(148)	17(3.5)	133(182)	110(56.2)	6(0.41)	24(4.5)	61(15)	2(0.08)	27(3.8)	21(2.7)
Armandia brevis[2] - 14	4(0.33)	6(0.74)	3(0.23)	1(0.06)	3(0.23)	1(0.06)	3(0.23)	16(5.1)	0(0)	1(0.06)	5(0.23)	0(0)
Capitella capitata[2] - 15	18(5.4)	94(135)	65(41)	10(0.41)	82(49)	66(12.6)	20(2.1)	36(11.6)	66(49)	3(0.23)	36(7.1)	13(0.23)
Axiothella rubrocinta[2] - 16	0(0)	0(0)	2(0.08)	7(1.4)	7(1.1)	5(1.5)	0(0)	0(0)	0(0)	1(0.06)	1(0.06)	2(0.25)
Owenia fusiformis[2] - 17	0(0)	2(0.08)	7(0.72)	8(1.2)	4(0.49)	9(1.1)	0(0)	1(0.06)	1(0.06)	0(0)	0(0)	1(0.06)
Thelepus crispus[2] - 18	8(2.8)	27(8.9)	34(13.3)	8(0.50)	19(3.4)	52(37.7)	4(0.33)	4(0.33)	5(0.39)	2(0.08)	18(2.7)	18(6.2)

	Subarea 3A						Subarea 4A					
	Stratum 1			Stratum 2			Stratum 1			Stratum 2		
Species - Number	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
Harmothoe multisetosa - 1	0(0)	0(0)	0(0)	0(0)	1(0.06)	0(0)	0(0)	4(0.99)	3(0.23)	3(0.23)	2(0.08)	1(0.06)
Eulalia parvoseta - 2	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Gyptis brevipalpa[1] - 3	0(0)	1(0.06)	2(0.25)	3(0.06)	2(0.08)	0(0)	1(0.06)	5(0.89)	2(0.25)	3(0.55)	3(0.06)	3(0.06)
Ophiodromus pugettensis[1] - 4	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	2(0.25)	1(0.06)	2(0.25)	2(0.25)	0(0)	3(0.56)
Platynereis bicanaliculata - 5	0(0)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)	13(1.1)	1(0.06)	0(0)	8(0.17)	5(0.23)
Nephtys caeca - 6	0(0)	0(0)	0(0)	2(0.08)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Glycera capitata[2] - 7	4(0.33)	4(0.33)	1(0.06)	2(0.08)	4(0.17)	1(0.06)	0(0)	2(0.08)	2(0.08)	2(0.08)	5(0.39)	1(0.06)
Diopatra ornata - 8	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Lumbrineris bicirrata[2] - 9	11(2.5)	6(0.91)	6(2.2)	0(0)	4(0.49)	6(0.91)	77(0.7)	8(1.9)	17(9.3)	40(3.8)	13(0.22)	15(2.7)
Dorvillea japonica[2] - 10	10(0.70)	13(0.54)	6(0.91)	5(0.88)	23(0.54)	15(3.2)	9(1.7)	17(2.9)	7(0.39)	14(2.7)	14(12)	5(0.56)
Scoloplos pugettensis[2] - 11	46(0.40)	18(0.41)	29(0.70)	55(4.5)	31(0.70)	19(2.4)	5(0.88)	5(0.39)	9(1.7)	6(1.4)	8(0.33)	2(0.25)
Naineris quadricuspida[2] - 12	2(0.25)	6(0.41)	4(0.17)	1(0.06)	5(0.23)	2(0.08)	40(0.48)	0(0)	3(0.56)	5(0.88)	1(0.06)	1(0.06)
Cirratulus cirratus[2] - 13	1(0.06)	19(2.2)	28(1.4)	4(0.99)	9(2.5)	2(0.25)	187(3.1)	16(1.2)	94(2.2)	6(0.74)	24(1.1)	24(0.66)
Armandia brevis[2] - 14	6(0.41)	2(0.08)	0(0)	8(0.08)	7(1.4)	0(0)	2(0.25)	21(0.06)	1(0.06)	4(0.33)	12(1.3)	8(1.8)
Capitella capitata[2] - 15	9(2.7)	81(0.54)	97(1.5)	104(1.4)	52(1.1)	85(1.9)	35(3.2)	59(4.1)	41(1.2)	28(4.1)	104(1.1)	43(0.22)
Axiothella rubrocinta[2] - 16	0(0)	0(0)	1(0.06)	0(0)	2(0.25)	3(0.23)	0(0)	24(1.6)	13(0.38)	17(2.4)	17(2.7)	9(1.2)
Owenia fusiformis[2] - 17	2(0.08)	2(0.25)	4(0.17)	4(0.49)	0(0)	3(0.23)	0(0)	0(0)	0(0)	2(0.25)	5(0.56)	0(0)
Thelepus crispus[2] - 18	0(0)	3(0.23)	0(0)	0(0)	5(0.56)	2(0.08)	1(0.06)	19(2.2)	5(0.39)	1(0.06)	0(0)	8(0.83)

[1]Treated as one group in the statistical analysis.
[2]Used in the statistical analysis.

null hypotheses resulted in no decision. The data from Table 2 indicate that the apparent variation does occur in these two cases (stratum 1 in both subareas 2A and 4A) as well.

The homogeneity (2) of the polychaete assemblage between strata, in a given subarea, in a given season was also examined using chi-square tests ($\alpha = 0.05$, 12 df). Five of the 12 null hypotheses were rejected (i.e., subarea 4A in the winter, subareas 1B, 2A, and 3A in the spring, and subarea 1B in the summer). A no decision result was reached in the remaining cases.

Bivalves

The sampling data collected on the bivalve populations in Garrison Bay are given in Table 3. The data are organized as follows: 1) *Protothaca staminea*, *Venerupis japonica*, and *Saxidomus giganteus* were grouped as one into the Veneridae; 2) *Macoma inconspicua*, *M. irus*, and *M. nasuta* were grouped as one into the Tellinidae; 3) *Transennella tantilla*, *Clinocardium nuttalli*, *Mya arenaria*, and *Mysella tumida* were considered individually; and 4) *Macoma secta* was considered apart from the Tellinidae because of its usual occurrence in clean sandy environments.

The size and the number of sampling units in this study were generally inadequate for sampling most mature bivalves. As a consequence, hypotheses for small bivalves, such as *T. tantilla* and *M. tumida*, are best represented by the data in this study. Indeed, large densities of *T. tantilla* were found in all four subareas, with the largest numbers in subarea 3A, and *M. tumida* was found in large numbers only in subarea 4A.

The north-south bivalve distribution, as constructed from these data, is somewhat different from that found in the polychaetes. The data in Table 3 show that the subareas may be ranked in descending order with respect to the total numbers of individuals as follows: subareas 3A and 1B and subareas 2A and 4A are about the same. However, occasional seasonal reorderings do occur. The high densities in subarea 3A are probably due to the presence of large numbers of *T. tantilla*. In terms of the number of species present, subarea 1B generally ranks highest and the remaining three subareas are almost indistinguishable.

Differences in the bivalve distributions within a season, on like-numbered strata, and between subareas were examined using chi-square tests

TABLE 3.—Total number of individuals of the seven groups of common bivalves in four samples: W = Winter, Sp = Spring, Su = Summer. Numbers in parentheses are estimates of the variance of sample means.

	Subarea 1B						Subarea 2A					
	Stratum 1			Stratum 2			Stratum 1			Stratum 2		
Species or family - Number	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
Veneridae[1] - 1	1(0.06)	6(0.41)	3(0.23)	3(0.06)	7(1.1)	4(0.33)	2(0.06)	2(0.25)	4(0.17)	2(0.25)	3(0.23)	2(0.06)
Tellinidae[1] - 2	10(2.4)	3(0.06)	3(0.23)	17(1.7)	3(0.06)	8(0.17)	8(1.2)	5(0.06)	2(0.06)	10(0.74)	3(0.23)	7(0.40)
Transennella tantilla[1] - 3	4(0.99)	13(3.2)	0(0)	8(0.83)	11(5.8)	6(0.08)	6(0.74)	16(1.5)	10(0.74)	9(1.7)	6(1.4)	2(0.08)
Macoma secta - 4	4(0.33)	1(0.06)	2(0.08)	2(0.08)	0(0)	1(0.06)	0(0)	0(0)	2(0.25)	0(0)	0(0)	0(0)
Clinocardium nuttalli - 5	1(0.06)	2(0.25)	0(0)	1(0.06)	0(0)	1(0.06)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Mya arenaria - 6	0(0)	0(0)	1(0.06)	1(0.06)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Mysella tumida - 7	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)

	Subarea 3A						Subarea 4A					
	Stratum 1			Stratum 2			Stratum 1			Stratum 2		
Species or family - Number	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
Veneridae[1] - 1	3(0.06)	0(0)	1(0.06)	1(0.06)	2(0.08)	0(0)	6(0.08)	1(0.06)	6(0.41)	1(0.06)	4(0.50)	5(0.89)
Tellinidae[1] - 2	3(0.06)	10(0.41)	9(0.23)	13(0.72)	10(0.74)	10(0.41)	9(0.39)	12(0.83)	11(2.4)	11(0.06)	12(0.50)	7(0.72)
Transennella tantilla[1] - 3	23(6.0)	9(0.56)	69(128)	27(1.5)	3(0.23)	35(30)	5(0.88)	3(0.23)	2(0.08)	0(0)	1(0.06)	0(0)
Macoma secta - 4	1(0.06)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Clinocardium nuttalli - 5	0(0)	1(0.06)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Mya arenaria - 6	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Mysella tumida - 7	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	7(0.23)	4(0.17)	0(0)	12(1.1)	6(0.74)

[1]Used in the statistical analysis.

($\alpha = 0.05$, 6 df). All six of the null hypotheses (2) were rejected. Thus the bivalve distributions between subareas are different. To investigate the sources of this difference in distribution, the bivalve assemblage on similarly numbered strata, in all combinations of subarea pairs and season were examined using chi-square tests ($\alpha = 0.05$, 2 df). Nineteen of these 36 null hypotheses of homogeneity (2) were rejected. Thus, the bivalve distribution is not consistent in either time (season) or space (sample subareas).

The homogeneity (2) of the bivalve assemblage between the three seasons for a single stratum was examined using chi-square tests ($\alpha = 0.05$, 4 df). Four of the eight null hypotheses were rejected. The homogeneity (2) of the bivalve assemblage between strata, in a given subarea, in a given season was also examined using chi-square tests ($\alpha = 0.05$, 2 df). Two of the 12 null hypotheses were rejected. Thus, a definitive statement about the dependence between bivalve presence and season cannot be made. Furthermore, the differences between the strata of a single subarea are apparently minimal.

DISCUSSION

The sediment and macrofauna data collected in the Garrison Bay study were analyzed under the assumption of intrasample independence within each subarea (i.e., the contents of one sampling unit neither predicts nor influences the contents of any other unit). The assumption is based upon the homogeneity of macrofauna and sediment composition within study subareas. Macrofaunal homogeneity is defined here as meaning that all members of a given species on a given stratum are described by the same spatial probability distribution. Although specific probability distributions were not fit to the data, chi-square and Kolmogorov-Smirnov tests are legitimately applied to the sample data.

There are K different systematic samples, each of size n, that could be chosen (recall $N = nK$); one of these is selected at random. The sample mean of the ith such systematic samples, $\bar{y}_i$, and the population mean, $\bar{Y}$, are defined respectively as:

$$\bar{y}_i = \left(\sum_{j=1}^{n} y_{ij}\right)/n \text{ and}$$

$$\bar{Y} = \left(\sum_{i=1}^{K} \sum_{j=1}^{n} y_{ij}\right)/nK$$

where y_{ij} is the attribute of interest in the sample (e.g., the number of individuals of a given species in the jth sample). Since systematic sampling is a probability sampling scheme, a valid expression for the variance of the sample mean is

$$\text{var}(\bar{y}_i) = \left(\sum_{i=1}^{K} (\bar{y}_i - \bar{Y})^2\right)/K \qquad \text{(Sukhatme and Sukhatme 1970).}$$

Alternative expressions of this quantity have been derived (Cochran 1963). No difficulties arise in using any of these forms of var ($\bar{y}_i$) in theoretical studies, but in applications of systematic sampling, no reliable estimate of var ($\bar{y}_i$) is known from taking only one sample of size n from an area. This is a disadvantage of SSS. In practice, approximations to var ($\bar{y}_i$) are used as estimators of this statistic. The texts by Cochran (1963:224-227) and Sukhatme and Sukhatme (1970:369-370) present several methods to approximate var ($\bar{y}_i$) from a single systematic sample. However, if m (≥ 2) independent systematic samples (each of size n) are taken on the same stratum at the same time, an exact (as opposed to an approximate) estimate of var ($\bar{y}_i$) is possible. Letting $\bar{y}_i$ represent the sample mean from one of the m systematic samples, then

$$\text{var}(\bar{y}) = \sum_{i=1}^{n} (\bar{y}_i - \bar{y})^2/m(m-1)$$

$$\text{where } \bar{y} = \left(\sum_{i=1}^{m} \bar{y}_i\right)/m \qquad \text{(Sukhatme and Sukhatme 1970).}$$

In this study the estimate of the variance of the sample means was approximated by the variance calculated for a simple random sample (Cochran 1963). This is reasonable because of the within-area homogeneity of the sediment and macrofauna in each of the four study areas. Of course, it is preferable to take at least two independent systematic samples, each of size n.

Cochran (1963) discussed the difference in precision between random and systematic sampling based on the results of these methods upon certain types of population data. Special attention should be given to data which is either inherently periodic or subject to a periodic input, e.g., tidal forces. Under these circumstances, K must be carefully selected. Periodic variation in the north-south direction in Garrison Bay is considered to be unlikely.

The use of SSS allows strata to be placed at tidal heights where experimental interest is focused. Thus, samples may be taken at fixed tidal levels as

in FLTS and statistically valid estimates of means and variances on a stratum found. Furthermore, no greater physical effort is required in SSS than in FLTS. SSS also provides a method to quantify species-presence gradients. Hence, SSS is free of some of the disadvantages of FLTS while maintaining the advantages often ascribed to FLTS plans.

There is a sediment gradient in the bay in the sense of a gradual increase in coarseness (silt to sand) south to north over the four areas for all seasons. Over all seasons, subarea 1B generally contained the largest number of bivalve species and, were it not for the abundance of *Transennella tantilla* (which is discussed later), subarea 1B would have the largest number of bivalves also. In addition, in almost all seasons subarea 1B contained the largest number of individuals and species of polychaetes. Thus, there is a distribution in bivalve and polychaete presence, from high density and species numbers to low as the sediment becomes more coarse. The sediment composition, as measured by average percentage composition by weight of various grain sizes, is a necessary factor to consider in predicting macrofauna population dynamics, but it is not a sufficient predictor by itself. This viewpoint is based on the necessity of employing qualitative information concerning the types of material retained by the 1.981-mm sieve (see Results section), and the role we attribute to the algae *Enteromorpha* sp. in the population dynamics of *T. tantilla* (see later discussion).

Newell (1965) found a higher number of microorganisms in areas composed of finer grades of sediment and an associated higher number of the deposit feeders (*Hydrobia ulvae* and *Macoma balthica*). He concluded that the large number of microorganisms was a result of the greater surface area of fine sediment grades which is related to the amount of organic nitrogen (protein) available to deposit feeders. The polychaete data from Garrison Bay, and subsequent statistical analyses, suggest that Newell's (1965) hypothesis can be extended to incorporate a statement about the biological effects of different sediment compositions in the presence of temporal heterogeneity. Recall that the sediment data show that subarea 4A, the most exposed subarea, experiences greater interseason fluctuations than does subarea 1B, the most sheltered subarea. Furthermore, the polychaete assemblage in subarea 1B shows the smallest seasonal fluctuation with regard to both total numbers of individuals and species as compared with subarea 4A. Subareas 2A and 3A also show smaller seasonal variations in both polychaete assemblage and sediment composition than does subarea 4A. All of this suggests that mixed fine sediment grades (silty areas) may act as insulators for certain infauna against seasonal stresses. That is, fine sediments with their larger total surface area to volume ratio retain larger quantities of nutrients (organic nitrogen) and hold more interstitial water. If the areas composed chiefly of fine sediment grades occur in the cul de sac of an embayment, where wave action is minimal, then these areas are more likely to retain larger numbers of individuals and species than other areas within the embayment. Thus, despite the periodic fluctuations in many environmental parameters of the intertidal zone, a constant sediment particle composition contributes to a high degree of environmental predictability. Slobodkin and Sanders (1969), Levinton (1972), and Gray (1974) considered aspects of the consequences of temporal predictability for deposit and suspension feeders.

The bivalves and polychaetes listed in Tables 2 and 3 represent both suspension and deposit feeders. Rhoads and Young (1970) advanced the hypothesis that animals of one trophic level modify the environment and affect the dynamics of members of another trophic level, and called it trophic group amensalism. They found suspension feeders in the subtidal to be generally restricted to sandy or firm mud bottoms, and deposit feeders to be more numerous in soft silty substrates. The polychaete results generally support this hypothesis. An exception noted by Young and Rhoads (1971) was the case in which it was hypothesized that tube-building polychaetes (both suspension and deposit feeders) make it possible for higher densities of bivalve and polychaete suspension feeders to coexist with deposit feeders in silty sediments because of their ability to bind particles together and thereby stabilize sediments. This hypothesis may be useful in explaining why suspension feeders, e.g., the tube builder *Owenia fusiformis* and the members of the Veneridae, are so numerous in subarea 1B, as well as why the tube building terebellid *Thelepus cripus*, a surface level deposit feeder, reaches its maximum density in subarea 1B. The combination of tube building coupled with the feeding behavior of suspension feeders may provide these organisms a survival advantage in this otherwise soft

silty area. Further studies are being conducted to develop hypotheses for Garrison Bay.

Newell's (1965) hypothesis does not appear to explain the abundance and apparent sediment preferences of *T. tantilla*. Maurer (1969) found *T. tantilla* to be ubiquitous in a bay with a sediment gradient similar to that of Garrison Bay, while attaining its greatest numbers in a region composed principally of finer sediment particle sizes. Excluding subarea 3A, similar results follow for *T. tantilla* in Garrison Bay. The increased abundance of this bivalve in the summer on both strata of subarea 3A indicates that the principal response of *T. tantilla* may be to something other than just sediment composition. The extensive covering of subarea 3A by a dense algal mat of *Enteromorpha* sp. is probably involved in the population explosion. *Transennella tantilla* would gain protection from some physiological stresses such as elevated temperatures and increased water evaporation by the sun and wind. Similar dense mats of *Enteromorpha* sp. were not found in the other three areas at the sampling times.

The polychaete assemblage in Garrison Bay is described by a distribution which is apparently sediment and season dependent. The limited data on the distribution of bivalves does not have the same patterns. Preliminary analyses from an investigation (Gallucci)[7] involving the collection of large numbers of bivalves in Garrison Bay substantiates the lack of a simple gradient relationship for bivalves. Life in a calcium carbonate shell seems to allow for greater independence from environmental fluctuations than life near the sediment surface without such a shell.

Although the effects of seasonal and sediment type variations are often evident, causal links must be established by the examination of specific factors, e.g., competition, predation, food availability and selection, salinity, and temperature. Toward this end, Hylleberg and Gallucci (1975) and Gallucci and Hylleberg (1976) have examined the role of food availability and sediment composition upon the growth of the deposit feeder *Macoma nasuta* in Garrison Bay. Garrison Bay daylight summer surface water temperatures are about 1°C higher in the closed end than in the open end (Gallucci, unpubl. data), and short stretches of intertidal areas sustain a subsurface freshwater runoff.

In this paper we have developed an appropriate sampling method for marine studies and the statistical machinery for testing certain relevant hypotheses. We have applied these methods in an intertidal study. The biological results pertain to sediment and animal gradients under seasonal change. Conclusions are based upon statistical comparisons in which the null hypothesis was rejected, tempered by extensive biological studies.

The data and results of the Garrison Bay study have obvious significance for shellfish culture. Factors such as the selection of sediment type in which to establish seed beds, interspecies associations, the season in which to make population assessments, and the sampling techniques should all be considered if sound management decisions are to be made.

[7]Gallucci, V. F. 1976. Bivalve community relationships as determined from age composition and growth rates. Unpubl. manuscr., 30 p.

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LITERATURE CITED

BIRNBAUM, Z. W., AND R. A. HALL.
1960. Small sample distributions for multi-sample statistics of the Smirnov type. Ann. Math. Stat. 31:710-720.

BLOOM, S. A., J. L. SIMON, AND V. D. HUNTER.
1972. Animal-sediment relations and community analysis of a Florida estuary. Mar. Biol. 13:43-56.

COCHRAN, W. G.
1963. Sampling techniques. 2d ed. John Wiley & Sons, Inc., N.Y., 413 p.

CONOVER, W. J.
1971. Practical nonparametric statistics. John Wiley & Sons, N.Y., 462 p.

FABER, J. A. J.
1972. Precision of sampling by dots for proportions of land use classes. Inst. Stat. (Raleigh, N.C.), Mimeogr. Ser. 773, 153 p.

FINNEY, D. J.
1948. Random and systematic sampling in timber surveys. Forestry 22:64-99.

GALLUCCI, V. F., AND J. HYLLEBERG.
1976. A quantification of some aspects of growth in the bottom-feeding bivalve *Macoma nasuta*. Veliger 19:59-67.

GRAY, J. S.
1974. Animal-sediment relationships. Oceanogr. Mar. Biol. Annu. Rev. 12:223-262.

HYLLEBERG, J., AND V. F. GALLUCCI.
1975. Selectivity in feeding by the deposit-feeding bivalve *Macoma nasuta*. Mar. Biol. (Berl.) 32:167-178.

LEVINTON, J.
1972. Stability and trophic structure in deposit-feeding and suspension-feeding communities. Am. Nat. 106:472-486.

LOESCH, J. G.
1974. A sequential sampling plan for hard clams in lower Chesapeake Bay. Chesapeake Sci. 15:134-139.

LOOSANOFF, V. L., AND F. D. TOMMERS.
1948. Effect of suspended silt and other substances on rate of feeding of oysters. Science (Wash., D.C.) 107:69-70.

MATERN, B.
1960. Spatial variation: Stochastic models and their application to some problems in forest surveys and other sampling investigations. Medd. Statens Skogsforkningsinst. 49:1-144.

MATTHIESSEN, G. C.
1960. Intertidal zonation in populations of *Mya arenaria*. Limnol. Oceanogr. 5:381-388.

MAURER, D.
1969. Pelecypod-sediment association in Tomales Bay, California. Veliger 11:243-249.

NEWELL, R.
1965. The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. Proc. Zool. Soc. Lond. 144:25-45.

OSBORNE, J. G.
1942. Sampling errors of systematic and random surveys of cover-type areas. JASA (J. Am. Stat. Assoc.) 37:256-264.

RAJ, D.
1968. Sampling theory. McGraw-Hill Book Co., N.Y., 302 p.

RHOADS, D. C.
1967. Biogenic reworking of intertidal and subtidal sediments in Barnstable Harbor and Buzzards Bay, Massachusetts. J. Geol. 75:461-476.

RHOADS, D. C., AND D. K. YOUNG.
1970. The influence of deposit feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28:150-178.

RUSSELL, H. J., JR.
1972. Use of a commercial dredge to estimate a hardshell clam population by stratified random sampling. J. Fish. Res. Board Can. 29:1731-1735.

SAILA, S. B., AND T. A. GAUCHER.
1966. Estimation of the sampling distribution and numerical abundance of some mollusks in a Rhode Island salt pond. Proc. Natl. Shellfish. Assoc. 56:73-80.

SANDERS, H. L.
1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. Limnol. Oceanogr. 3:245-258.

SEN, A. R., J. TOURIGNY, AND G. E. J. SMITH.
1974. On the line transect sampling method. Biometrics 30:329-340.

SKELLAM, J. G.
1958. The mathematical foundations underlying the use of line transects in animal ecology. Biometrics 14:358-400.

SLOBODKIN, L. B., AND H. L. SANDERS.
1969. On the contribution of environmental predictability to species diversity. Brookhaven Symp. Biol. 22:82-95.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry: The principles and practice of statistics in biological research. W. H. Freeman & Co., San Franc., 776 p.

SUKHATME, P. V., AND V. B. SUKHATME.
1970. Sampling theory of surveys with applications. Iowa State Univ. Press, Ames, 452 p.

VASSALLO, M. T.
1969. The ecology of *Macoma inconspicua* (Broderip & Sowerby, 1829) in central San Francisco Bay. Part I. The vertical distribution of the *Macoma* community. Veliger 11:223-234.

WARME, J. E.
1971. Paleoecological aspects of a modern coastal lagoon. Univ. Calif. Publ. Geol. Sci. 87, 131 p.

WIESER, W.
1959. The effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. Limnol. Oceanogr. 4:181-194.

YOUNG, D. K., AND D. C. RHOADS.
1971. Animal-sediment relations in Cape Cod Bay, Mass. I. A transect study. Mar. Biol. (Berl.) 11:242-254.

SIZE COMPOSITION AND GROWTH OF YOUNG ROCK CRAB, *CANCER IRRORATUS*, ON A ROCKY BEACH IN MAINE[1]

JAY S KROUSE[2]

ABSTRACT

Monthly hand collections of small rock crab, *Cancer irroratus*, were made from an intertidal zone in East Boothbay, Maine, from June 1972 through April 1975. An analysis of size and sex frequencies indicated: 1) young-of-the-year crabs (≤5 mm carapace width) entered the intertidal area in late summer-early fall and remained there through the second fall with a resultant width range between 15 and 40 mm; 2) a deceleration and/or cessation of growth in winter; 3) an emigration of crabs >40 mm carapace width from the intertidal area associated with declining winter temperatures and/or behavioral changes; 4) sex ratios approximated a 1:1 relationship; and 5) small male and female rock crabs (<60 mm carapace width) had a common growth rate.

While searcing beneath the rocky substrate of an intertidal zone for juvenile American lobster, *Homarus americanus* Milne Edwards, whose early distribution and abundance is generally unknown, I discovered numerous small rock crab, *Cancer irroratus* Say, burrowed under the rubble. Because rock crab is a valuable commercial species as well as an important food source of lobsters (Ennis 1973), I believe it important to describe the distribution of young crabs in their natural environment along with other life history information (size structure, sex ratio, and growth).

METHODS

Rock crabs were carefully hand collected about once a month during extreme low slack tides from the intertidal zone of Grimes Cove, East Boothbay, Maine (Figure 1). The rocky substrate of this unsheltered seaward cove consists of rocks of assorted sizes intermingled amongst areas of bedrock, sand, and pulverized shells. By using large boulders as landmarks, it was possible to sample consistently the same general area near the low water mark. Unfortunately, for various reasons, samples could not be obtained for all months of the study.

After two biologists concurrently expended 1 h gathering crabs, their catches were immediately returned to the laboratory where sex and carapace width (distance between the two most posterior notches on the anterolateral border) to the nearest millimeter were recorded. The sex of crabs <10 mm carapace width (CW) was determined under a dissecting microscope.

Width-frequency histograms were compiled by 2-mm increments for rock crabs caught each month from June 1972 through April 1975.

RESULTS AND DISCUSSION

Size Composition and Seasonal Distribution

Since there were no discernible differences in size distribution between male and female crabs, the data for sexes were combined in monthly width-frequency histograms (Figure 2). This similarity in size composition of male and female crabs <60 mm CW suggested a common growth rate for both sexes up to this size, unlike the marked size disparity of larger male and female rock crabs (>60 mm CW) caught in commercial lobster traps which was primarily attributed to a decrease in the growth rate of females after the onset of sexual maturity (Krouse 1972).

Modal groups, which most likely represented one or, perhaps, more molt classes, were quite conspicuous in each of the monthly histograms. However, due to extensive overlapping of modes I was unable to quantitatively follow these modal groupings from month to month for purposes of estimating mortality rates.

Inspection of monthly histograms revealed that young-of-the-year crabs (recently metamorphosed from megalops to first crab, ≤5 mm CW) initially

[1]This study was conducted in cooperation with the National Marine Fisheries Service, NOAA, Department of Commerce, under Public Law 88-309, as amended, Commercial Fisheries Research and Development Act, Project 3-153-R.

[2]Maine Department of Marine Resources, West Boothbay Harbor, ME 04575.

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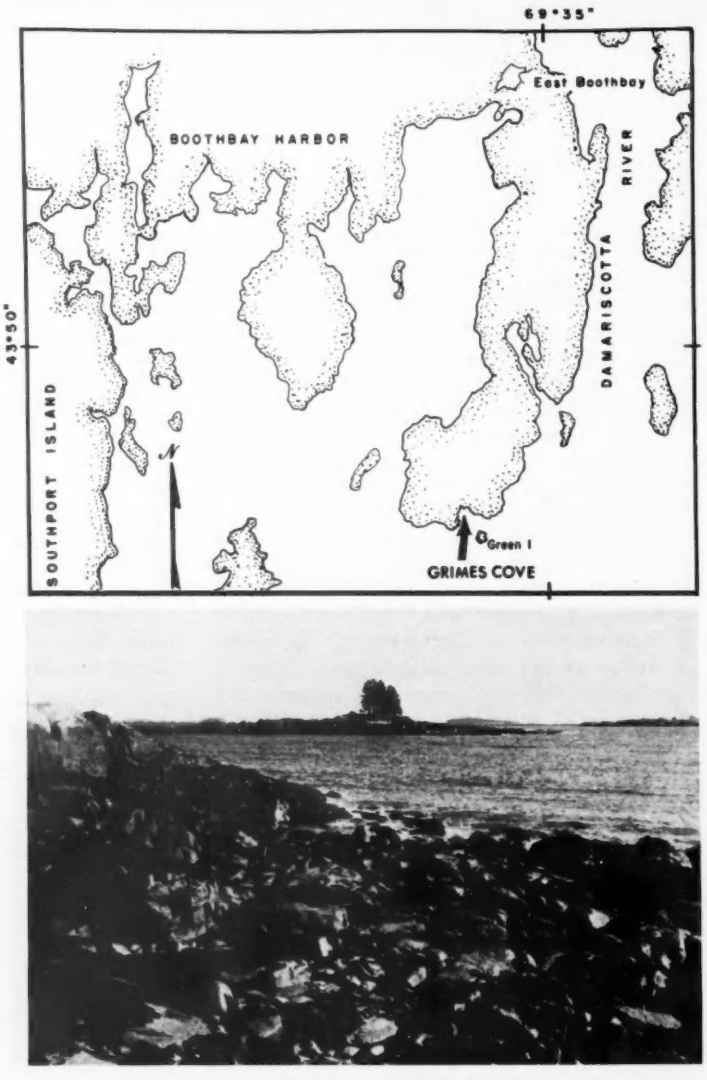

FIGURE 1.—Chart of Boothbay region with a seaward view at low tide of the intertidal beach of Grimes Cove, East Boothbay, Maine.

appeared during September 1972 and late August 1973 and 1974. This seasonal appearance of young crabs agreed with earlier observations of female rock crabs hatching their eggs in late spring and early summer in Maine waters (Krouse 1972) and the culture work of Sastry (1970) which demonstrated that 40 - 60 days are required for rock crabs to develop through the pelagic larval stages to the first crab stage at 15°C and a salinity of 30‰.

Histograms showed a gradual upward progression of the first modal grouping (comprised of young-of-the-year crabs, <10 mm CW) from August through December 1974, while distributions from January through April 1975 revealed relatively little change (Figure 2). This apparent cessation of growth was further supported by sighting very few, if any, cast exoskeletons and/or soft-shelled crabs while sampling during the winter. At other times of the year, when crabs were growing, numerous recently cast shells and/or shedders were readily observed. In spring when growth resumed, the percentages of in-

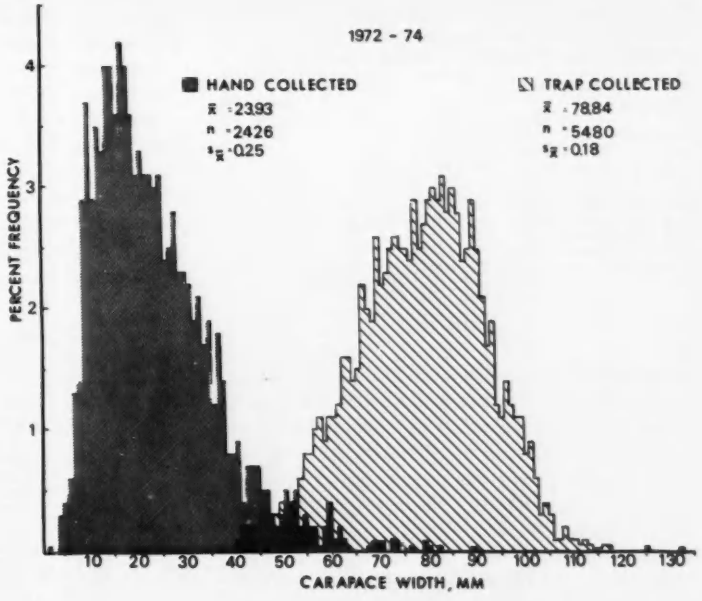

FIGURE 2.–Width-frequency distributions for rock crabs collected monthly by hand at an intertidal area in East Boothbay, Maine, 1972-75.

dividuals <10 mm CW began to diminish progressively until late summer when young-of-the-year crabs once again settled to the bottom (Table 1).

Rock crabs >40 mm CW were decidedly less abundant during the fall and winter (Table 1). In fact, not a single crab >50 mm CW was captured from January through April (Figure 2). This seasonal shift in size distribution suggested that crabs >40 mm CW moved seaward from the intertidal zone with declining temperatures. Jeffries (1966) reported that *C. irroratus* moved from Narragansett Bay, R.I., in winter to the deeper and warmer ocean waters. Conversely, in southern waters during the late fall and winter, rock crabs moved into Delaware Bay (Winget et al. 1974) and inshore waters of Virginia (Shotton 1973; Terretta 1973) as the water temperatures fell within a preferred range.

Aside from the apparent thermal effects and/or behavioral changes on the seasonal displacement of these large crabs from the intertidal zone, this movement may also be associated with the larger crabs' physical ability to emigrate with ease from an area of low temperature. In addition, the size of these crabs may inhibit their ability to find suitable burrows in the littoral zone necessary to afford protection from the often tempestuous winter sea. Jeffries (1966) stated that *C. irroratus* was not well suited for burrowing into coarse bottom.

TABLE 1.–Percentage of rock crabs of two carapace widths in monthly samples for 1972-75.

Month	≤10 mm (%)	≥ 40 mm (%)	Month	≤10 mm (%)	≥ 40 mm (%)
Jan.	39.6	0	Aug.	1.6	16.6
Mar.	47.4	2.6	Sept.	13.7	12.7
Apr.	34.8	2.7	Oct.	31.4	6.7
May	32.8	2.9	Nov.	40.9	8.0
June	7.8	8.5	Dec.	40.7	3.7
July	2.4	8.8			

Sex Ratio

Ratios of males to females for each of the monthly samples ranged from 0.60:1 to 1.57:1 (Table 2). The chi-square test revealed that only sex ratios of catches of July and August 1973 deviated significantly ($P = 0.05$) from a 1:1 relationship. Thus I concluded that sex ratios of the intertidal catches approximated a 1:1 relationship (1,353 males: 1,376 females); whereas, rock crabs larger than 50 mm CW collected in traps near Boothbay Harbor, Maine, showed disproportionate sex ratios which varied by season and locality (Krouse 1972). It appears that these disparate sex ratios were primarily a function of the onset of sexual maturity which subsequently altered the growth rate and seasonal distribution of male and female crabs.

TABLE 2.–Sex ratios of the monthly collections of rock crabs taken intertidally in East Boothbay, Maine, 1972-75. Sex ratios that deviated significantly ($P = 0.05$) from 1:1 are marked *.

Mo.	1972 M:F	1973 M:F	1974 M:F	1975 M:F	Mo.	1972 M:F	1973 M:F	1974 M:F	1975 M:F
Jan.	—	1.27:1	—	0.96:1	Sept.	0.89:1	—	1.57:1	—
Mar.	—	—	—	1.23:1		0.71:1			
Apr.	—	0.60:1	0.76:1	1.08:1	Oct.	0.68:1	—	1.23:1	—
May	—	1.07:1	1:1	—	Nov.	—	—	0.96:1	—
June	1.02:1	0.95:1	1.03:1	—	Dec.	—	—	0.93:1	—
July	1.25:1	1.55:1*	0.82:1	—	Total	0.98:1	0.99:1	0.95:1	1.08:1
Aug.	1.01:1	0.71:1*	0.86:1	—					
		0.87:1							

Growth

Carapace width prior to shedding was plotted against the new carapace width after shedding for 45 crabs that molted while captive in the laboratory. This relationship was fitted by the method of least squares using the simple linear equation $Y = a + bX$, where Y = postmolt CW, X = premolt CW, and a and b were constants. Analysis of covariance, which was used to test homogeneity of regression coefficients, revealed no statistical differences between growth increments of males and females, so all data were pooled. The calculated equation for crabs ranging from 9 to 48 mm CW was $Y = 0.566 + 1.247X$. This relation was similar to Cleaver's (1949) constants ($a = 0.57$; $b = 1.23$) calculated for Dungeness crab, *C. magister*, juveniles (5-91 mm CW).

Based on the relationship between premolt vs. postmolt and measurements of cultured post-larval crabs (stages I-V) obtained from Herbert C. Perkins, formerly of the National Marine Fisheries Service, West Boothbay Harbor, Maine, I estimated sizes for instars I-XIII (Table 3). Sizes for instars above XIII were not computed because of the inherent uncertainties of extrapolating beyond the data range. If we assume that Maine rock crabs begin to attain maturity about 60 mm CW (Krouse 1972; Scarratt and Lowe 1972) and if as suggested by Butler's (1961) work with *C. magister* the premolt vs. postmolt relationship changes with the onset of sexual maturity, then sizes for instars beyond XIII (53 mm CW) are inadequately described by the aforementioned regression.

Because the increments of growth (24.3-28.3%) for post-larval crabs (instars III-V) cultured in the laboratory were appreciably less than those growth increments (29.2 to 30.6%) for instars VI-VIII of the captive wild crabs, widths for instars II-XIII were estimated by the empirical value (2.6 mm CW) for stage I and then the subsequent stages were calculated with the linear regression (Table 3). Instar sizes calculated by this procedure were larger (about one instar size greater) than those sizes based on empirical data for stages I-V and predicted by regression for instars VI-XIII, e.g., instar V (estimated by regression) = 9.5 mm and instar VI (other method) = 9.6 mm. For purposes of this study, those instar sizes calculated with the empirical post-larval data were favored.

TABLE 3.–Comparison of instar sizes of rock crabs. For one group, instars I-V represent actual measurements and instars VI-XIII are calculated by the relationship $Y = 0.566 + 1.247X$; for the other group, instar I is an actual measurement and the remaining instars are estimated from the aforementioned equation.

	I-V: Actual measurements VI-XIII: regression values		Regression values	
Instar	Carapace width (mm)	Increase (%)	Carapace width (mm)	Increase (%)
I	2.6		2.6	
II	3.7	42.3	3.8	46.4
III	4.6	24.3	5.3	39.5
IV	5.9	28.3	7.2	35.3
V	7.4	25.4	9.5	32.5
VI	9.6	30.3	12.4	30.6
VII	12.5	30.6	16.1	29.2
VIII	16.2	29.2	20.6	28.2
IX	20.8	28.2	26.3	27.4
X	26.4	27.4	33.3	26.8
XI	33.5	26.8	42.1	26.4
XII	42.4	26.4	53.0	26.0
XIII	53.4	26.0	66.7	25.7

An attempt was made to objectively assign size with age by correlating instar size with the monthly width-frequencies (Figure 2). As mentioned previously, post-larval crabs (2-5 mm CW) first entered the sampling area in August or September after having hatched in late spring or summer and having developed through the larval stages during the remainder of the summer. Size distributions for April 1974 through April 1975 revealed first entry of young-of-the-year crabs in August followed by subsequent growth of young crabs until about January when growth ceased and this modal group stabilized at about 4-20 mm CW (instars III-IX). This wide size range is best explained by varying hatching and settling dates whereby some crabs entered the population perhaps 1 to 2 mo later than the rest. These crabs settled to the bottom when temperatures were likely to be declining; thus these individuals experienced little growth until the following spring.

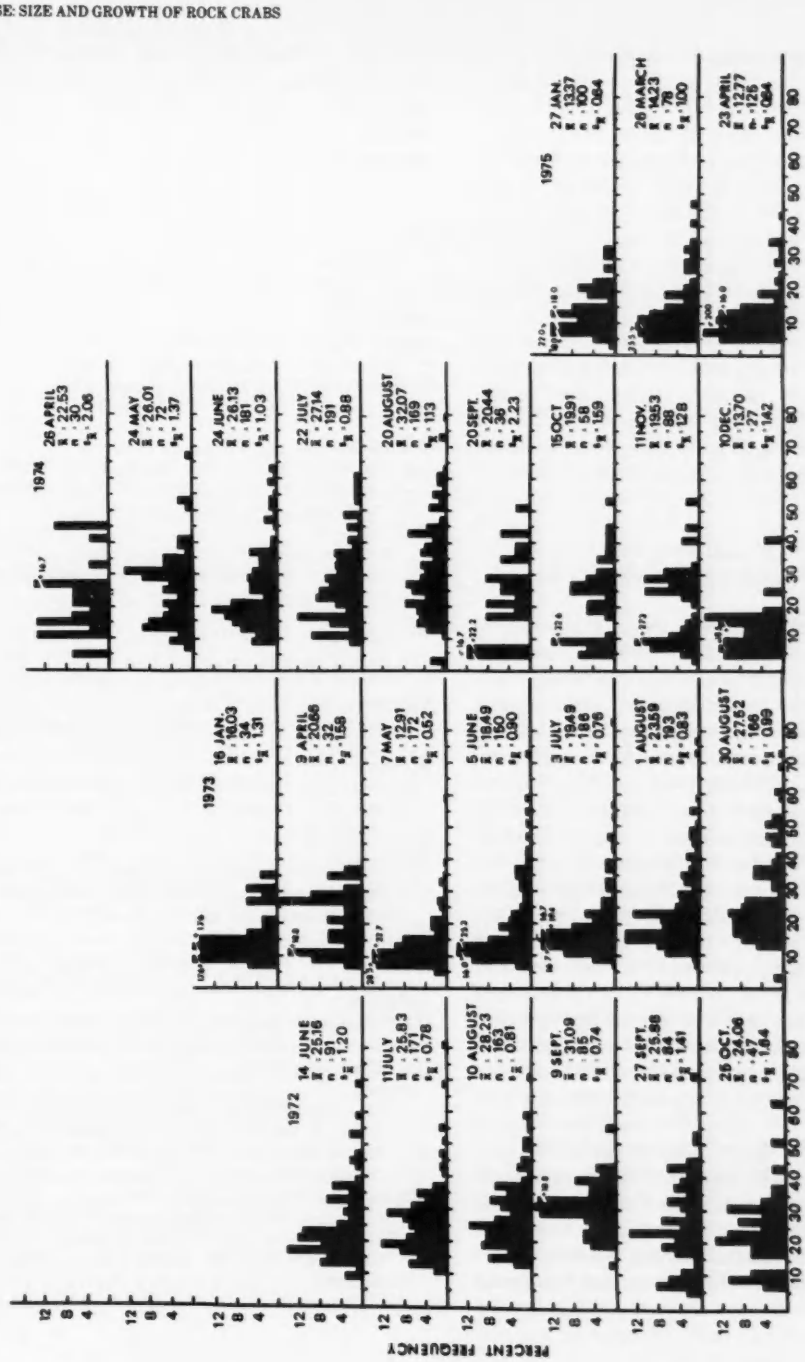

FIGURE 3.—Width-frequency distributions for rock crabs collected by hand in an intertidal area and by trap in the Boothbay region, 1972-74.

When growth resumed in late spring and summer, only a few juveniles (previous year's young-of-the-year) were <10 mm CW (stage VI). Unfortunately, the overlapping of modes prevented any objective determination of the upper limit of this second modal grouping that represented the juvenile crabs. Nevertheless, several of the monthly distributions (September-October 1972 and August 1973) exhibited an upper limit around 40 mm CW for this second modal grouping (Figure 2).

Although it was not possible to make precise determinations of age and growth from information of this study, the data suggest that young-of-the-year crabs ranged in size from about 4 to 20 mm CW (instars III-IX) and the juveniles in their second fall ranged from approximately 15 to 40 mm CW (instars VIII-XII).

Hand-Collected Vs. Trap-Caught Crabs

Prior to sampling small crabs in the intertidal zone, our rock crab work was based on incidental catches of crabs with wire lobster traps (25.4-×25.4-mm mesh) in the Boothbay Harbor area (Krouse 1972). Histograms plotted by 1-mm increments for 2,426 hand-collected and 5,480 trap-caught crabs (1972-74) graphically revealed marked differences in size composition of the catches for these two methods of capture (Figure 3). Average width for hand-collected crabs was 23.9 mm and 78.8 mm for trapped crabs. Even though these two complementary modes of capture sampled a broad range of sizes (2-133 mm CW), many crabs between 40 and 60 mm CW eluded either type of collection. This scarcity of crabs between 40 and 60 mm CW can be attributed to: 1) selectivity of traps against sizes <60 mm CW (based on Figure 3, crabs <70 mm CW were not fully vulnerable to the gear), and 2) movement of crabs >40 mm CW from the intertidal zone in association with low winter temperatures and possible behavioral changes with size. Scarratt and Lowe (1972) reported that small rock crabs (<65 mm CW) in the Northumberland Strait, Gulf of St. Lawrence, inhabited rocky areas, whereas larger crabs left the rocky substrate for sand and mud bottoms. Jeffries (1966) noted that *C. irroratus* dwelled chiefly on sand in the Narragansett Bay–the type of bottom this species is adapted to because of its well developed walking and burrowing abilities.

ACKNOWLEDGMENTS

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LITERATURE CITED

BUTLER, T. H.
1961. Growth and age determination of the Pacific edible crab *Cancer magister* Dana. J. Fish. Res. Board Can. 18:873-891.

CLEAVER, F. C.
1949. Preliminary results of the coastal crab (*Cancer magister*) investigation. Wash. Dep. Fish., Biol. Rep. 49A:47-82.

ENNIS, G. P.
1973. Food, feeding, and condition of lobsters, *Homarus americanus*, throughout the seasonal cycle in Bonavista Bay, Newfoundland. J. Fish. Res. Board Can. 30:1905-1909.

JEFFRIES, H. P.
1966. Partitioning of the estuarine environment by two species of *Cancer*. Ecology 47:477-481.

KROUSE, J. S.
1972. Some life history aspects of the rock crab, *Cancer irroratus*, in the Gulf of Maine. J. Fish. Res. Board Can. 29:1479-1482.

SASTRY, A. N.
1970. Culture of brachyuran crab larvae using a re-circulating sea water system in the laboratory. Helgoländer wiss. Meeresunters. 20:406-416.

SCARRATT, D. J., AND R. LOWE.
1972. Biology of rock crab (*Cancer irroratus*) in Northumberland Strait. J. Fish. Res. Board Can. 29:161-166.

SHOTTON, L. R.
1973. Biology of the rock crab, *Cancer irroratus* Say, in the coastal waters of Virginia. M. A. Thesis, Univ. Virginia, Charlottesville, 72 p.

TERRETTA, R. T.
1973. Relative growth, reproduction and distribution of the rock crab, *Cancer irroratus*, in Chesapeake Bay during the winter. M.A. Thesis, College of William and Mary, Williamsburg, Va., 104 p.

WINGET, R. R., D. MAURER, AND H. SEYMOUR.
1974. Occurrence, size composition and sex ratio of the rock crab, *Cancer irroratus* Say and the spider crab, *Libinia emarginata* Leach in Delaware Bay. J. Nat. Hist. 8:199-205.

MINIMUM SWIMMING SPEED OF ALBACORE, *THUNNUS ALALUNGA*

RONALD C. DOTSON[1]

ABSTRACT

Measurements of density and pectoral lifting area of albacore, *Thunnus alalunga*, were made and compared with those previously described for yellowfin tuna, *Thunnus albacares*; bigeye tuna, *Thunnus obesus*; and skipjack tuna, *Katsuwonus pelamis*. Albacore have densities within the range of yellowfin tuna of similar size. The pectoral lifting area of albacore was always greater than skipjack tuna but similar to yellowfin tuna and bigeye tuna for fish less than 70 cm long. Larger albacore had increasingly larger fins than did the other species.

Minimum speed necessary for hydrostatic equilibrium of albacore was calculated and compared at 50 and 80 cm fork lengths to values calculated for the species above. Albacore minimum speeds were slower than those for skipjack tuna, similar to those of yellowfin tuna, and greater than those of bigeye tuna. Density variations of albacore, attributed to fat content and gas bladder volume, significantly affected estimates of minimum speed. Calculated speeds were slower than those estimated for albacore tracked at sea or estimated from tag returns.

Albacore tuna, *Thunnus alalunga* (Bonnaterre), being negatively buoyant in seawater, must swim continuously to maintain their position in the water column. The albacore's long pectoral fins help to compensate for their negative buoyancy by providing lift, thus lowering the swimming speed necessary to maintain hydrostatic equilibrium.

A model developed by Magnuson (1970) proposes that the minimum swimming speed of a scombrid fish is set by the necessity to maintain hydrostatic equilibrium rather than to provide adequate gill ventilation. When the lift provided by the pectoral fins necessary to compensate for the weight of the fish in water is estimated, the corresponding swimming speed can be considered the minimum necessary for the maintenance of hydrostatic equilibrium. This model was used by Magnuson (1973) to compare minimum speeds of several species of scombrid fishes that differed in pectoral lifting area, body shape, body density, and the presence or absence of a gas bladder.

The purpose of this paper is to 1) estimate the minimum swimming speed of albacore; 2) compare the minimum swimming speed of albacore with those for other scombrids; and 3) compare calculated minimum swimming speeds of albacore with swimming speeds estimated from sonic tracking of albacore at sea and from long distance tag returns.

MATERIALS AND METHODS

To compute the minimum swimming speed with Magnuson's (1970) model, it is necessary to determine the mass of the fish, the lifting area, the density of the seawater, and the density of the fish. As the peduncle keels probably provide negligible lift (Magnuson 1973), they are excluded in the computation of minimum speeds.

To determine the mass of albacore, 477 specimens caught between long. 130° and 140°W and lat. 30° and 40°N during June 1974 were weighed to the nearest gram on a magnetically dampened pan balance and their fork lengths recorded to the nearest millimeter. Specimens were weighed and measured within 15 min after capture.

A regression $\ln M = \ln a + b(\ln L)$, where M is mass in grams and L is fork length in millimeters, was fitted to the length-mass data. The resultant equation was

$$M = 4.514 \times 10^{-5} L^{2.8746} \quad (1)$$

with 95% confidence limits on the exponent from 2.8245 to 2.9246.

The total pectoral lifting area (A) is equal to the projected surface area of the pectoral fins plus the projected body area between them, due to their analogy to wings in which the pressure distribution set up by the wings extends across the fuselage (Magnuson 1970). The pectoral lifting area was determined by tracing the outline of the

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detached left pectoral fin on a piece of paper having a thickness of 0.25 mm. The outlined form was cut out and weighed to the nearest 0.01 g on a balance. Projected area was calculated from a ratio of the paper weights to a standard, and doubled to account for the other pectoral fin.

Thirty-three 100 cm^2 pieces of the paper were measured with a micrometer and weighed to determine the affect of variations in paper thickness and cutting accuracy on the calculations. The thickness of the paper varied less than 1% around the mean, and cutting accuracy varied by $\pm 2\%$. The affect on calculations of pectoral lifting area was, therefore, assumed to be negligible.

The projected body area between the pectoral fins was determined by multiplying the body width at the pectorals by the width of the pectoral fin at its point of attachment to the body as measured on the fresh fish. Pectoral fin lifting areas were determined for 42 fish caught in the area described above and for 8 larger fish caught off Oregon in October 1974. The following relationship was established between the lifting area (A in square centimeters) and the fork length (L in millimeters):

$$A = 4.7351 \times 10^{-6} L^{2.6727}. \quad (2)$$

Albacore observed cruising under the baitboat kept their pectoral fins extended continuously at a sweepback angle of approximately 45°. The tips of an albacore's fins are also not rigid, and the effect of this on the lifting capacity of the fin has been ignored.

A water density (D_e) of 1.025 g/ml was determined from temperature and salinity data from the offshore region described above. This also equalled the mean water density within the nearshore albacore fishery.

Fish densities were determined for three groups of fish: group 1–seven fish caught during June 1974 in the offshore region; group 2–14 fish caught 60 miles south of San Diego on 23 July 1975, presumably 2 wk after they appeared off the coast; and group 3–37 fish caught on 13 September 1975 in the same region as group 2 but assumed to have been near the coast for 2 mo.

The group 1 fish were frozen immediately after capture and, when returned to the laboratory, thawed and weighed on a spring balance while suspended in seawater to determine the density of the fish in seawater (D_f).

Fish from groups 2 and 3 were weighed in seawater on a pan balance immediately after capture and their densities in seawater determined.

VARIATIONS IN DENSITY

The density of group 1 fish (Figure 1) is well within the range of those determined for fresh fish of similar size indicating that freezing and thawing probably had negligible affect on density determinations. All specimens were caught on or near the surface by jigline or rod and reel, and there was no difference in density attributable to one method of capture over the other.

Rough estimates of the development of the gas bladders of 21 fish in group 3 were made immediately after other measurements were completed. In specimens less than 56 cm FL (fork length), the bladder was small (approximately 1 cm wide and 8 or 9 cm long) and contained little or no gas. In specimens 60 to 70 cm FL, the bladder was approximately 5 cm wide and 16 cm long and filled with gas to a depth of 4 or 5 cm. Fish over 80 cm FL had bladders approximately 30 cm long and 10 cm in diameter which occupied a large volume of

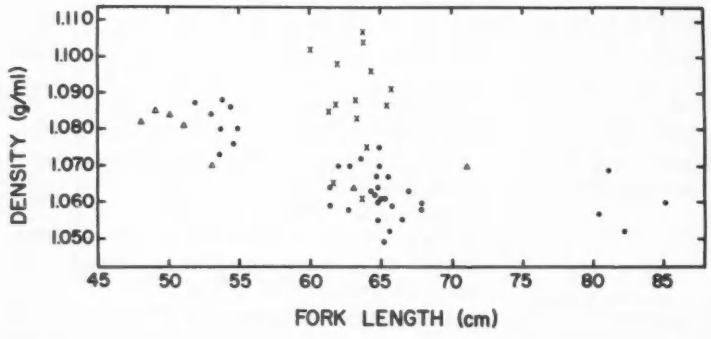

FIGURE 1.–Computed densities for three groups of albacore: group 1 (triangles); group 2 (crosses); and group 3 (dots). See text for explanation of groups.

the gut cavity. All developed gas bladders appeared full with two exceptions, and these may have been damaged during capture or dissection.

Seven albacore caught in September with fork lengths of 63 to 68 cm were examined to determine the effect of the gas bladder on density. Gas was removed from the bladder by a cannula (inside diameter = 1 mm) which was inserted through the ventral surface of the body while the fish was submerged in seawater, and the fish was then weighed while still submerged. The mean density increase with gas extraction was 0.007 g/ml (Table 1). Although this is probably a conservative estimate, the difference in density calculated before and after gas removal is used as the effect of the gas bladder on fish density. In an albacore less than 56 cm FL, the small gas bladder is not expected to affect density whereas the large and fully developed gas bladder of albacore greater than 80 cm FL should reduce density to a greater extent than was measured on the smaller fish above.

Densities of group 2 fish were considerably higher than those of similar size fish in groups 1 and 3 (Figure 1). Seasonal variations in density due to changes in fat content have been described for other pelagic species by Aleev (1963). Mass estimates were calculated from the length for each fish in all three groups using Equation (1), and compared with the observed values. The mean of the observed values for group 2 fell 403 g below the estimate from the regression line, ranging from 172 g greater to 999 g less. Because fish in group 2 had apparently just migrated into the area of capture, presumably from the central or western Pacific, the loss in mass was assumed to have been caused by the utilization of fat during migration. Group 1 would not yet have utilized this fat, and group 3 is assumed to have added fat by feeding in the rich coastal waters.

The densities in group 2 were recomputed on the assumption that the mass difference between the individuals and the regression curve is attributed to fat loss. An equation was developed by Magnuson (1970) relating the density (D_f) of a scombrid without a gas bladder to the percentage (P) of the total body weight that is fat. The equation

$$D_f = 1.100 - 0.0017\,P \qquad (3)$$

was used to recompute densities for the fish in group 2. The effect of the gas bladder on density was assumed to be 0.007 g/ml because fish in group 2 were in the same size range as the above fish for which gas bladder measurements were taken. This value was added to the observed density and the percentage body weight in fat calculated. The difference in mass (assumed to be fat loss) of each individual was then added and new densities determined with the increased percentage of body fat. The density effect of the bladder was subtracted from this value to yield a density adjusted for fat loss. When determining fat content in the fish, the density effect of the bladder was taken into account, except for those fish with measured densities greater than 1.100 g/ml, which is the level Magnuson (1970) chose as the density for a scombrid without a gas bladder. Fish with densities greater than 1.100 were assumed to have empty or damaged gas bladders, and the density difference due to the gas bladder was subtracted from the recomputed density.

Recomputed densities of group 2 are plotted in Figure 2 with the measured densities of groups 1 and 3. The close fit of the recomputed densities appears to support the assumption that fat content and gas bladder volume can account for the disparity in densities observed for group 2 in the original data. Density values are, therefore, expected to vary considerably depending on the development and condition of the gas bladder and the fat content of the fish when it is caught.

DETERMINATION OF MINIMUM SPEED

To estimate the minimum speed for hydrostatic equilibrium, it is necessary to calculate the amount of lift a fish must produce. The lift (L_f) required by a scombrid to attain hydrostatic equilibrium, expressed in dynes, is determined from the relation (Magnuson 1970)

$$L_f = M\left[\left(1 - \frac{D_e}{D_f}\right)980\ \mathrm{cm/s^2}\right]. \qquad (4)$$

When the lift is assumed to be provided solely by the pectoral fins, and the coefficient of lift for the pectorals is assumed to be 1.0, then the equation for minimum swimming speed becomes (Magnuson 1970)

$$V = \left[\frac{L_f}{D_e/2(A)}\right]. \qquad (5)$$

Calculations of minimum swimming speed from

TABLE 1.–Density changes in albacore following gas bladder deflation and resultant effect on estimation of minimum speed.

Characteristic	Albacore no. 1	2	3	4	5	6	7	Mean
Fork length (mm)	627	643	646	648	653	679	679	654
Density with gas bladder (g/ml)	1.058	1.063	1.062	1.055	1.061	1.060	1.058	1.059
Density without gas bladder (g/ml)	1.063	1.069	1.068	1.058	1.067	1.067	1.071	1.066
Change in density due to gas bladder (g/ml)	0.005	0.006	0.006	0.003	0.006	0.007	0.013	0.007
Minimum speed with gas bladder (cm/s)	45.0	48.6	48.7	44.5	49.8	47.3	47.9	47.4
Minimum speed without gas bladder (cm/s)	47.9	52.2	52.4	46.5	53.9	51.7	56.3	51.6
Change in minimum speed due to gas bladder (cm/s)	2.9	3.6	3.7	2.0	4.1	4.4	8.4	4.2

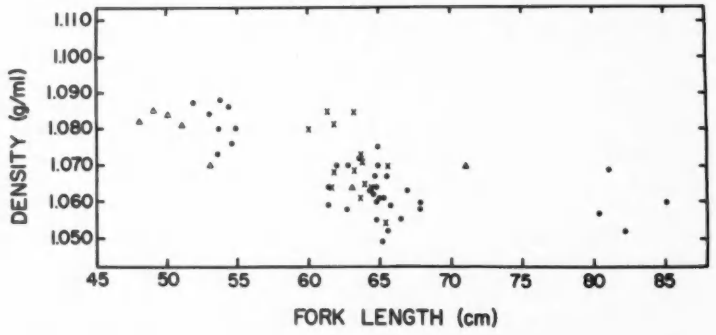

FIGURE 2.–Computed densities for three groups of albacore with group 2 densities (crosses) recomputed after correction for fat loss. Recomputation of group 2 densities is explained in the text.

this equation assume 100% extension of the pectoral fins.

The mass of the fish (M) and the lifting area (A) can be calculated using Equations (1) and (2), respectively. The density of the environment (D_e) is 1.025 g/ml. If we use M = 2,540 g, D_f = 1.082 g/ml, A = 77.4 cm^2 for a 50-cm fish, the calculated minimum speed V is 54 cm/s.

Density variations due to fat content and gas bladder volume can affect the minimum swimming speed necessary to maintain hydrostatic equilibrium. For a 65-cm albacore, a loss of 10% of its body weight in fat would result in a 10% increase in minimum speed. Loss or emptying of the gas bladder results in an 8% increase in minimum speed. Minimum speeds calculated from data on fish with full gas bladders and in good condition are therefore considered to be the minimum obtainable while retaining hydrostatic equilibrium.

COMPARISON OF MINIMUM SPEEDS OF FOUR SCOMBRIDS

Minimum speeds were calculated for albacore; yellowfin tuna, *Thunnus albacares*; bigeye tuna, *T. obesus*; and skipjack tuna, *Katsuwonus pelamis*, at fork lengths of 50 and 80 cm. The speeds are given in Table 2 with the density, mass, and pectoral lifting area used in the computations.

The minimum swimming speed of albacore decreases from 57 cm/s when they are 50 cm FL to 45 cm/s at 80 cm FL. The decrease is a direct result of the allometric growth of the pectoral fins (Yoshida 1968) and the gas bladder (Gibbs and Collette 1966). The gas bladder of albacore does not have significant development when the fish is less than 55 cm long, but has considerable volume at a fish length of 65 cm, and apparent complete development when the fish has reached 80 cm FL (data, this paper). Combined with the increasing length of the pectoral fins, the result is a relatively

TABLE 2.–Estimated minimum speeds of four species of scombrids at fork lengths of 50 and 80 cm. The mass of the fish (M), pectoral lifting area (A), and density of the fish (D_f) used in the computations are also given.

Species	Fork length (cm)	M (g)	A (cm^2)	D_f (g/ml)	V (cm/s)
Thunnus alalunga[1]	50	2,588	77.40	1.082	57
	80	9,992	271.04	1.056	45
Thunnus obesus[2]	50	2,429	96.63	1.047	32
	80	10,825	233.80	[3]1.030	21
Thunnus albacares[4]	50	2,501	91.56	1.087	55
	80	10,338	220.50	1.050	47
Katsuwonus pelamis[4]	50	2,539	47.88	1.090	78
	80	12,567	137.20	1.096	107

[1]Data from present paper.
[2]M, A, and D_f from Magnuson (1973).
[3]Extrapolated value.
[4]M calculated from Chatwin (1959), A and D_f from Magnuson (1973).

abrupt drop in minimum speed between 60 and 70 cm FL (Figure 3).

Albacore and yellowfin tuna have very similar densities (Table 2), but the pectoral fins of albacore are smaller in young fish (Gibbs and Collette 1966), increasing very rapidly in size as the fish mature (Figure 4). Thus, small albacore have a faster minimum swimming speed than small yellowfin tuna, and albacore over 65 cm have a slower minimum swimming speed than the same size yellowfin (Table 2, Figure 3) assuming similar fat content and gas bladder development.

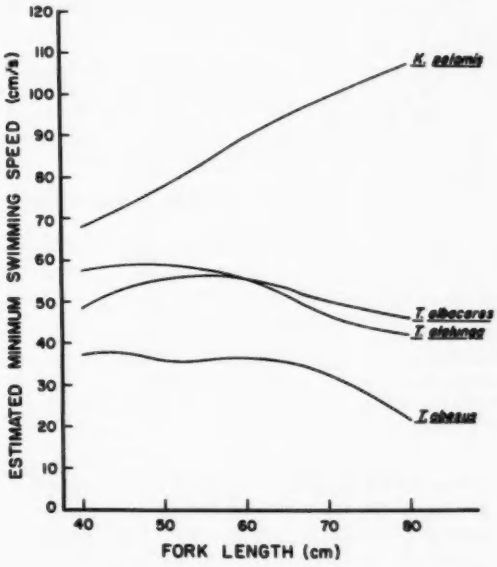

FIGURE 3.—The estimated minimum swimming speed of four scombrids using Magnuson's (1970) model for hydrostatic equilibrium.

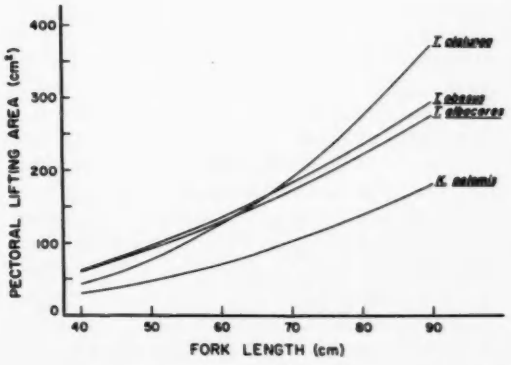

FIGURE 4.—Regression curves for pectoral lifting area (A) versus fork length. Curves for *Thunnus obesus*, *T. albacares*, and *Katsuwonus pelamis* are from Magnuson (1973). The curve for *T. alalunga* is from Equation (2) in the text.

Because bigeye tuna have a larger gas bladder than albacore and also have large pectoral fins, both of which grow allometrically (Gibbs and Collette 1966), their estimated minimum swimming speed is only half that of albacore at both 50 and 80 cm in length (Table 2).

The minimum swimming speed necessary for hydrostatic equilibrium of 50-cm albacore is 70% that of 50-cm skipjack and only 40% when each is 80 cm long (Table 2). Unlike albacore, skipjack have no gas bladder and always have small, short pectoral fins; therefore, skipjack tuna must swim faster as their mass increases in order to maintain hydrostatic equilibrium (Figure 3).

In Table 2 and Figure 3, density values for bigeye tuna were extrapolated beyond observed values and those of albacore were chosen from "fat" fish; therefore, actual values shown may not be exact, but the gross relationships among species are expected to hold true.

FIELD ESTIMATES OF ALBACORE SWIMMING SPEEDS

During August 1972, the National Marine Fisheries Service in cooperation with the American Fishermen's Research Foundation tagged six albacore with sonic tags and tracked their movements off the coast of Monterey Bay, Calif. (Laurs et al. 1972).[2]

Mean speeds observed during sonic tracking of three fish near 85 cm fork length were 95 cm/s during daylight hours and 62 cm/s during the night. These speeds are higher than the calculated minimum of 42 cm/s for a fish this size.

Each of two tagged albacore approximately 80 cm long, which were caught after a trans-Pacific migration, had a computed minimum or straight line speed (based on great circle route and time free) of 26 nautical miles/day or 55 cm/s (Japanese Fisheries Agency 1975). The calculated minimum speed of 45 cm/s is remarkably close to the estimated minimum migration speed of these two

[2]Laurs, R. M., H. S. H. Yuen, and J. H. Johnson. 1972. Study of the small-scale movements of albacore using ultrasonic tracking techniques. *In* Report of Joint National Marine Fisheries Service-American Fishermen's Research Foundation Albacore Studies Conducted during 1971 and 1972, p. 54-72. Unpubl. Rep. SWFC, NOAA, La Jolla.

fish but could be an artifact of many interacting processes and events.

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LITERATURE CITED

ALEEV, YU. G.
1963. Function and gross morphology in fish. Izd. Akad. Nauk SSSR, Mosc., 245 p. (Translated from Russian by the Israel Program Sci. Transl., 1969, 268 p.; available U.S. Dep. Commer, Natl. Tech. Inf. Serv., Springfield, Va., as TT 67-51391.)

CHATWIN, B. M.
1959. The relationships between length and weight of yellowfin tuna (*Neothunnus macropterus*) and skipjack tuna (*Katsuwonus pelamis*) from the Eastern Tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 3:305-352.

GIBBS, R. H., JR., AND B. B. COLLETTE.
1966. Comparative anatomy and systematics of the tunas, genus *Thunnus*. U.S. Fish. Wildl. Serv., Fish. Bull. 66:65-130.

JAPANESE FISHERIES AGENCY.
1975. Report of tuna tagging for 1974. [In Jap.] Pelagic Res. Sec., Far Seas Fish. Res. Lab., 18 p.

MAGNUSON, J. J.
1970. Hydrostatic equilibrium of *Euthynnus affinis*, a pelagic teleost without a gas bladder. Copeia 1970:56-85.
1973. Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombroid and xiphoid fishes. Fish. Bull., U.S. 71:337-356.

YOSHIDA, H. O.
1968. Pectoral fin length of juvenile albacore. Copeia 1968:625-626.

PRODUCTION OF FRY AND ADULTS OF THE 1972 BROOD OF PINK SALMON, *ONCORHYNCHUS GORBUSCHA*, FROM GRAVEL INCUBATORS AND NATURAL SPAWNING AT AUKE CREEK, ALASKA

JACK E. BAILEY, JEROME J. PELLA, AND SIDNEY G. TAYLOR[1]

ABSTRACT

Production of fry and adults of the 1972 brood of pink salmon, *Oncorhynchus gorbuscha*, at Auke Creek, Alaska, was compared between a gravel incubator hatchery and natural spawning. Natural production in the creek above the hatchery weir (estimated from hydraulic sampling) was 73,900 fry (SE: 32,800) from an estimated initial seeding of 934,065 eggs (SE: 42,811) for a survival rate of 0.079 (SE: 0.035). An estimated total of 579,000 unfed fry (SE: 25,296) were released from the hatchery for a comparable survival rate of 0.743 (SE: 0.047). Exactly 84,000 of the hatchery fry and 5,500 of the creek fry were released after being marked by clipping fins. All adults returning to the weir were examined for marks, and some additional marks were recovered from sport and commercial fishermen; 667 marked hatchery fish and 74 marked creek fish were recovered. Estimated survival of hatchery fry to returning adult was only 0.0079 (SE: 0.0003) equal to 0.59 (SE: 0.071) the corresponding estimate of 0.0135 (SE: 0.0016) for creek fry, which suggests that hatchery fry were inferior to creek fry in the marine environment; however, hatchery fry emigrated seaward 2 wk earlier than creek fry and may have encountered less favorable marine conditions. Survival from eggs to returning adult stage was 5.50 times (SE: 2.59) higher for hatchery fry than for creek fry because of much greater survival from egg to fry in the hatchery; the difference is not statistically significant. Hatchery fry were generally shorter but heavier than creek fry and emigrated seaward at a slightly earlier stage of development. No differences in size or time of return of adults could be traced to the incubation environment from which they came.

The level of harvest of pink salmon, *Oncorhynchus gorbuscha*, in Alaska in the 1970's (Seibel and Meacham 1975) has been about one-ninth the level of the 1930's (Kasahara 1963). This decline, in view of recent advances in salmon hatchery systems (Bams 1972), might be countered by large-scale artificial propagation of salmon fry to supplement natural spawning. As a first step toward developing systems for enhancing or rehabilitating the depleted stocks, the National Marine Fisheries Service, Northwest Fisheries Center Auke Bay Fisheries Laboratory and the Alaska Department of Fish and Game agreed in August 1971 to begin testing a gravel incubator hatchery on Auke Creek near Juneau in southeastern Alaska.

Auke Creek was selected because it is accessible and has a fish weir and a dependable water supply from nearby Auke Lake. Lake water is especially desirable for hatcheries in Alaska because the water temperature generally remains above freezing (3°-4°C). However, lake water has at least one disadvantage—it has a different seasonal temperature pattern than most of the streambed waters where pink salmon eggs normally incubate. Bams (1972) avoided the problem of temperature differences by collecting hatchery water from beneath the streambed, but this is not always feasible in Alaska because of the severe freezing conditions encountered at many potential hatchery sites. This report on the 1972 brood pink salmon at Auke Creek compares hatchery production and natural production in regard to 1) survival from eggs to emergent fry, fry to returning adults, and eggs to returning adults; 2) size, stage of development, and emergence timing of fry; and 3) size and time of return of adults returning to Auke Creek from hatchery and creek fry.

MATERIALS AND METHODS

A heated building (7.3 by 13.4 m) provided space for a water filter and ultraviolet purifier; incubators; instruments for measuring temperature and oxygen; equipment for censusing, sampling, and marking fry; and instruments for measuring and counting adult salmon. The building was located on Auke Creek near a fish-counting weir at the head of tide where eggs could be collected from

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returning adult salmon. The hatchery water supply came from nearby Auke Lake. The eggs were incubated to the eyed stage in Heath[2] incubators and then transferred to gravel incubators to complete development.

Water Filter and Purifier

The water filter and ultraviolet purifier system supplied treated water to one-half of the hatchery incubators; the rest were supplied with untreated water. The filter was rated to remove particles 10 μm in diameter or larger. The purifier was designed to give a minimum dosage of 35,000 $\mu W \cdot s/cm^2$ at 2,537 Å. The water treatment had no apparent beneficial effect.

Natural Spawning

From 4 August to 21 September 1972, 1,768 adult pink salmon entered the fish counting weir. About 55%, 459 females and 527 males, were released to spawn above the weir. The rest were kept for fecundity counts and hatchery spawn source. Ten females from which we obtained fecundity counts were treated as a simple random sample in later analysis, although no serious effort was made to assure randomness of selection. Average fecundity in this sample was 2,035 eggs/female (SE: 93.27). This estimate agreed closely with 2,023 eggs/female from an inventory of eggs obtained from the 386 females used as the hatchery spawn source after a rough correction for eggs retained. Most pink salmon released above the weir spawned in a 297-m section of stream between the weir and Auke Lake. Fewer than 20 adults spawned in Lake creek above Auke Lake. The alevin population of Auke Creek was estimated 20-21 March 1973 with a hydraulic pump census (McNeil 1964).

Collection and Eyeing of Eggs

Eggs for seeding incubators were obtained from the Auke Creek pink salmon run 8 August through 22 September 1972. These dates cover nearly the entire run, thereby assuring representation of all parts of the run in the next generation. Eggs were collected from 386 females (about 45% of the females in the spawning run) in the manner described by Bailey and Taylor (1974). Malachite green treatments, 15 ppm. for 1 h, were used at weekly intervals between 17 August and 19 October to control fungus growth until eyed eggs were removed from the Heath trays.

Raising Eyed Eggs to Fry Stage

The eyed eggs were raised to the fry stage in four gravel incubators (Bams 1970) designated A, B, C, D (Table 1). The incubators measured 1.2 by 1.2 by 1.2 m and used a system of perforated pipes and horizontal layers of graded gravel to achieve uniformity of upwelling flow through the eggs and gravel. Flow to A, B, and C was initially set at 75 liters/min and to D at 79 liters/min. Incubators A, B, and C were loaded with an estimated 150,000 eggs (SE: 1,030) each and incubator D with an estimated 158,000 eggs (SE: 1,085) (Table 1). Therefore each incubator initially contained 2,000 eggs per liter/min.

Iron bacteria sheaths and a flocculent iron precipitate accumulated in the incubators. The material seemed to accumulate as rapidly in incubators receiving filtered and irradiated water as in those receiving untreated water. The intended water flow through the incubators receiving treated water could not be maintained. Flow through incubator C had dropped from the desired 1.26 liters/s to 0.88 liter/s 18 December 1972, and flow through incubator B had dropped to 0.95 liter/s 3 January 1973. Flow through these incubators was maintained at 0.63-1.07 liters/s for the rest of the incubation period. The full 1.26 liters/s was maintained at all times in the two incubators receiving untreated water, probably because the hydraulic head on the untreated water supply was about twice the head on the treated water.

The estimates of numbers of eggs seeded in each incubator were determined by the method of Burrows (1951). Through an oversight, records of

TABLE 1.—Operating conditions in four gravel incubators seeded with eyed pink salmon eggs, Auke Creek, 1972. For each incubator the volume of substrate and eggs was 1.246 m^3.

Incubator	Number eggs	Water flow (liters/min)	Type of water treatment
A	150,000	75	Untreated
B	150,000	75	Filtered and ultraviolet treated
C	150,000	75	Filtered and ultraviolet treated
D	158,000	79	Untreated

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

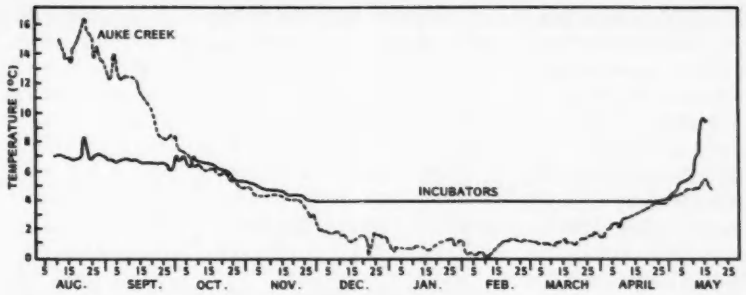

FIGURE 1.–Temperatures in gravel incubators and in surface water of Auke Creek, 8 August 1972 through 17 May 1973.

the procedure were of insufficient detail to estimate the precision of the initial seedings. Variances of these initial seedings were estimated from data obtained in recent years, 1974 and 1975. This source of error was determined to be negligible in later calculations.

Eggs were fertilized on the following schedule: incubator A, 4-31 August; B, 4 August to 8 September; C, 11-17 September; and D, 17-21 September.

Water Temperatures

We measured temperatures daily with a mercury thermometer (to the nearest 0.1°C) in Auke Creek and in the incubators from the time the first eggs were collected until the fry left the creek. While eggs were being collected (8 August to 22 September 1972), water in Auke Creek was warmer than water in the incubators (Figure 1). The creek water was cooler than the incubator water from 9 October throughout the rest of the incubation period, which ended when the fry emerged.

Oxygen Levels

Oxygen concentrations in the water supply to the hatchery and in effluents from the incubators were measured to the nearest 0.01 mg/liter by the Winkler method. Oxygen was measured at weekly intervals from shortly after eyed eggs were seeded (9 November 1972) until the fry began to emerge (23 March 1973). Oxygen content of the water supplied to the incubators decreased steadily–from 9.6 mg/liter (73% saturation) on 22 November 1972 to 7.8 mg/liter (59% saturation) on 23 March 1973 (Figure 2). Oxygen in effluents from gravel incubators decreased from 9.3 mg/liter (71% saturation) to 6.7 mg/liter (51% saturation) during the same period.

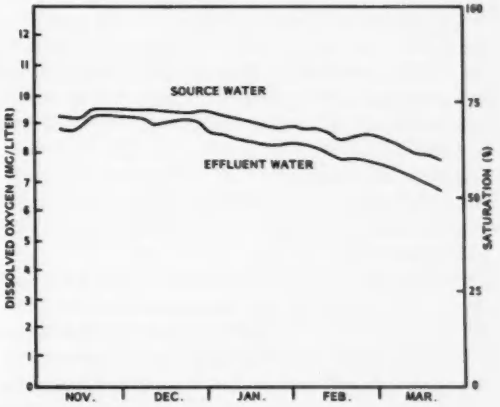

FIGURE 2.–Dissolved oxygen levels in source water and effluent water of gravel incubators at Auke Creek Hatchery, 9 November 1972 through 23 March 1973.

Counting and Processing Fry

We collected emigrating creek fry and hatchery fry to measure and mark, to determine time of migration, and to estimate abundance of hatchery fry. Two 0.91- by 0.91-m fyke nets with floating live-boxes were used to index the daily emigration of creek fry and to collect fry for a mark and recovery experiment. The daily counting of fry as they emerged from gravel incubators and the collection of fry for fin clipping and measuring was expedited by passing the incubator effluents over a cone-shaped sampling device[3] and then through a second sampling device consisting of a set of five parallel troughs. The first device provided small subsamples of fry from which total numbers emerging could be estimated; the second

[3]A blueprint for the cone-shaped fish sampler was supplied by the Washington Department of Fisheries.

device separated a larger subsample from the total numbers for marking.

We calibrated the cone device as a sampler with which to estimate total numbers of emerging fry from the incubators. Inspection of the relationship of total fry emigrating from an incubator (y) plotted against fry retained by the sampler (x) on 24 occasions indicated a constant ratio (straight line through the origin) with increasing variation at higher subsampler counts (Figure 3). Consequently, the average of the 24 ratios (y/x) available from the calibration study is taken as the slope estimate (Snedecor 1956: 153-156) and was calculated as 24.537 (SE: 1.072). The major portion of the fry passed the cone sampler and were then routed through the parallel troughs, one of which emptied into a holding tank and four of which emptied into the hatchery drain and then into Auke Creek. With these two devices we captured about one-fourth of the gravel incubator fry each day without impeding the seward migration of the other three-fourths.

Twice weekly, samples of 50 fry from each gravel incubator and the fyke nets were preserved in 5% Formalin. The preserved fry were allowed to stand for 6 wk before lengths were measured to the nearest millimeter and wet weights to the nearest milligram. An index to stage of development (Bams 1970) of the fry was computed from the formula

$$K_D = \frac{10\sqrt[3]{\text{weight in milligrams}}}{\text{length in millimeters}}.$$

This index is used only on unfed fry to indicate the relative yolk content. It is not a condition factor.

Weighted means and variances of pooled data were computed on the basis of the fraction of the migrant fry represented by each sample. Statistical comparisons were made of lengths, wet weights, and developmental index as follows:

$$\bar{Y}_W = \Sigma W_i \bar{Y}_i$$

where $\bar{Y}_W$ = weighted mean
$\bar{Y}_i$ = observed mean measurement in ith period
W_i = proportion of run leaving in ith period from index sampling, and

$$V(\bar{Y}_W) = \sum_{i=1}^{n} W_i^2 V(\bar{Y}_i)$$

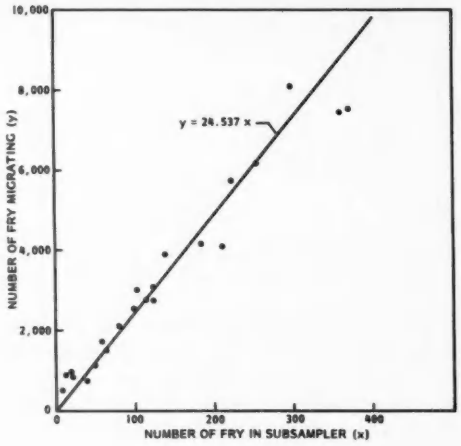

FIGURE 3.—Relation of number of fry migrating to number of fry in subsampler. Each point represents one sample.

where $V(\bar{Y}_W)$ = variance estimate of weighted mean
$V(\bar{Y}_i)$ = sample variance of estimated mean in ith period
n = number of periods sampled.

Technicians marked hatchery fry by clipping the adipose and left ventral fins and creek fry by clipping the adipose and right ventral fins. Before marking, the fry were anesthetized in a solution of 1:7,500 MS-222 (Tricaine methanesulfonate) buffered with sodium bicarbonate to pH 6.1-6.4; the solution was kept cool in a water table and recirculated to keep the oxygen content high. Surgical iris scissors were used to excise fins under a 3× magnifying lens. Technicians marked an average of about 200 fry/h on this study, whereas technicians marked about 400 fry/h on a similar study in Canada (R. A. Bams pers. commun.). Samples of fry from each technician were examined several times daily to ensure that the correct fins were excised as close to the body as possible. All marked fry were released at 1130 h the same day they were marked; most of the unmarked fry that had left the incubator or the stream at the same time had migrated seaward 24 h earlier. Dead fry remaining in the release tank were counted each morning. The immediate mortality from marking was less than 0.1% for both hatchery and creek fry. Totals of marked fry released were 84,000 from the hatchery and 5,500

from the creek. The daily numbers of marked fry released from the hatchery and the creek were roughly proportional to the respective migrations of fry from these two sources. There was a slight bias toward marking too few fry during the first half of the migration, but the bias was in the same direction and magnitude on both types of fry.

Less than 1% of the creek fry died in the fyke net and floating live-box, indicating slightly greater physical abuse for marked creek fry than marked hatchery fry.

Recovery of Marked Adults

Returning 1972 brood adults were counted at the weir in Auke Creek in the summer of 1974; some adult salmon were anesthetized and measured. Mideye-to-tail-fork lengths were measured to the nearest millimeter and weights to the nearest 0.01 kg.

Analysis of Survival

Survival probabilities from egg to fry and fry to returning adult are estimated from estimates of initial number of eggs, fry produced, and returning adults. Ratios of these survival estimates are used to compare survival of hatchery and creek salmon. Variances of survival and estimates of ratios of these survival estimates were approximated by the delta method (Deming 1943; Paulik and Robson 1969). Finite population correction factors were ignored in variance calculations; changes in variance estimates would have been insignificant.

Estimation of survival from marking requires special argument. The expected total unmarked returns from hatchery and creek fry combined is

$$T = Us + U's'$$

where U and U' are initial numbers of unmarked fry from the creek and hatchery respectively, and s and s' are the probabilities of survival of the two unmarked groups at sea. Marking increases mortality. If the probability of survival from marking is τ and identical for both groups, the probabilities of survival from both causes are $s\tau$ and $s'\tau$ for creek and hatchery fry respectively. The expected total return of the unmarked fry had they been marked, T', is

$$T' = Us\tau + U's'\tau.$$

The ratio of T' to T is τ. Therefore, we estimate survival from marking from estimates of T and T' as

$$\hat{\tau} = \hat{T}'/\hat{T}.$$

The expectation T is estimated by the total unmarked recoveries to the weir. The expectation T' is estimated from appropriate combinations of estimates of numbers of unmarked creek and hatchery fry and estimates of marine survival of marked fry of both groups.

Total variation among incubators in estimated survival from egg to fry is divided into three sources: 1) Underlying variation due to heterogeneity of genetic composition of pink salmon and environmental conditions among incubators, 2) binomial variation within incubators, and 3) sampling error in estimation of numbers of eggs and fry. We imagine an unobserved universe of survival probabilities s with mean $\bar{s}$ has been sampled randomly by our study; four members were drawn, each applying to one of our incubators. Actual survival within an incubator varies from its associated probability of survival due to binomial variation; instead of a fraction s surviving, the actual fraction is $\hat{s}$. This actual rate was not observed; rather, we estimated $\hat{s}$ by $\hat{\bar{s}}$, the ratio of estimated fry to estimated eggs.

Total variance of estimated survival among incubators, σ_t^2, is defined by

$$\sigma_t^2 = \underset{3}{E}(\hat{\bar{s}} - \bar{s})^2$$

where $\underset{3}{E}$ denotes the expectation operation over the three sources of variation.

This expression may be rewritten as

$$\sigma_t^2 = \underset{3}{E}[(\hat{\bar{s}} - \hat{s}) + (\hat{s} - s) + (s - \bar{s})]^2.$$

After completing the square and evaluating the expectations of the terms, we find

$$\sigma_t^2 = \sigma_1^2 + \sigma_2^2 + \sigma_3^2$$

where $\sigma_1^2 = \underset{1}{E}(s - \bar{s})^2$, the variance of underlying survival probabilities among incubators; $\sigma_2^2 = \underset{2}{E}(\hat{s} - s)^2$, the average binomial variance; $\sigma_3^2 = \underset{3}{E}(\hat{\bar{s}} - \hat{s})^2$, the average variance due to errors in estimates of fry and eggs; $\underset{1}{E}$ denotes the expectation operation over the first source of variation; and $\underset{2}{E}$ denotes the expectaton operation over the first two sources of variation.

Our experiment provides four unobserved selections from the underlying probabilities of survival, four estimates of binomial variation, and four estimates of variance in estimated survival due to errors in estimates of eggs and fry. Averages of the four estimates for the second and third sources are used to estimate σ_2^2 and σ_3^2. The sample variance of $\hat{s}$ is used to estimate σ_T^2. The estimate of σ_1^2 is obtained by subtraction.

RESULTS

First, we evaluate the effectiveness of the Auke Creek Hatchery by comparing survival of hatchery and creek fishes at different life stages: egg to emergent fry, fry to returning adult, and egg to returning adult. Next we estimate survival from marking. Then we compare size, stage of development, and emergence timing of hatchery fry with creek fry. Finally, we compare size and time of return of hatchery fish and creek fish as adults.

Survival from Egg to Fry

We estimated survival from potential egg deposition to fry for creek fry as the ratio of an estimate of the alevins in the spawning area of the creek above the weir in the spring of 1973 (just before emergence) to an estimate of the potential egg deposition. Because 459 females spawned in the stream above the weir, we estimate potential egg deposition as (459)(2,035) = 934,065 [SE: (459)(93.27) = 42,811 eggs].

On 20 and 21 March 1973, we determined the number of live alevins in each of 86 0.1-m^2 units of a simple random sample from the 8,600 such units making up the spawning area above the weir. The average number of alevins per unit was 8.593 (SE: 3.814). Hence, total live alevins in the spawning area was estimated to be (8,600)(8.593) = 73,900 alevins [SE: (8,600)(3.814) = 32,800 alevins].

Survival to time of sampling is estimated as the ratio of estimated total alevins to estimated potential egg deposition or 73,900/934,065 = 0.079 (SE: 0.035).

In the gravel incubators, estimated survival from live egg to fry was calculated as the ratio of estimated total emigrants to initial numbers of live eggs. The sums of the daily numbers of fry in subsamples from the four incubators were as follows: (A) 5,960; (B) 5,792; (C) 5,153; and (D) 6,692. Total emigrations from the incubators and corresponding standard errors were estimated using the calibration results: (A) (5,960)(24.537) = 146,240 fry [SE: (5,960)(1.072) = 6,389 fry]; (B) 142,118 (SE: 6,209); (C) 126,439 (SE: 5,524); and (D) 164,202 (SE: 7,174). The grand total of fry emigrating was 579,000 (SE: 25,296).

Estimates of survival from live eyed eggs to fry and the standard errors of these estimates were as follows: (A) 146,240/150,000 = 0.975 (SE: 0.043); (B) 0.947 (SE: 0.041); (C) 0.843 (SE: 0.037); and (D) 1.039 (SE: 0.045). The estimate for incubator D is not feasible, but since it lies within a standard error of the feasible range, we do not suspect errors in data recording or calculations. The mean of the survival estmates was 0.951, and the sample variance of the estimates was 0.00667.

This variance estimate is divided into three components—$\hat{\sigma}_1^2$, $\hat{\sigma}_2^2$, $\hat{\sigma}_3^2$—representing variation in underlying survival probabilities, binomial variation, and variation due to errors in estimating eggs and fry respectively. The estimates are as follows: $\hat{\sigma}_1^2 = 0.00493$, $\hat{\sigma}_2^2$ is negligible, and $\hat{\sigma}_3^2 = 0.00174$. Therefore, most of the total variance of survival estimates among the four incubators seems due to variation in underlying survival within the incubators rather than binomial variation or variation in egg or fry counts.

The incubator survival rates are from live eyed egg to fry. The creek survival rate is from potential egg deposition to fry. To make the survival rates comparable, we adjust the incubator survival to that from potential egg deposition to fry. The proportion of potential egg deposition which develops to the eyed stage in the hatchery is estimated as the ratio of total estimated eyed eggs obtained from the 386 females artificially spawned to estimated potential egg deposition by the females, or 614,000/785,510 = 0.782 (SE: 0.036). The adjusted incubator survival rate from potential egg deposition to fry is (0.782)(0.951) = 0.743 (SE: 0.047).

Survival from Fry to Returning Adult

Although most of the marked returning adults were recovered at the weir in Auke Creek below their point of origin, some were recovered from sport and commercial fishermen and from the intertidal spawning area of Auke Creek (Table 2). Total recoveries from all sources were used to estimate relative survival from fry to returning adult: 667 of the marked hatchery fish and 74 of the marked creek fish were recovered. Estimated survival of hatchery fry to returning adults is

667/84,000 = 0.0079 (SE: 0.0003). Estimated survival of creek fry for the same period is 74/5,500 = 0.0135 (SE: 0.0016). Therefore, our estimate of relative survival of hatchery fish as compared to creek fish is 0.0079/0.0135 = 0.59 (SE: 0.071).

TABLE 2.–Source of recoveries ofmarked pink salmon adults originating from fry marked at Auke Creek in 1973.

Source of recovery	Origin of marks	
	Hatchery	Creek
Commercial fishery	4	1
Sport fishery	8	0
Intertidal area of Auke Creek	11	2
Auke Creek weir	644	71
Total	667	74

Survival from Egg to Returning Adult

While hatchery fry suffered greater losses than creek fry in the marine environment, their increased survival under the artificial conditions during incubation was compensating. Overall relative survival from potential egg deposition to returning adult can be estimated as the ratio of the products of survival from potential egg deposition to alevin and from fry to returning adult for hatchery and creek fry. The survival of hatchery fish relative to creek fish is

$$(0.743)(0.0079)/(0.079)(0.0135) = 5.50 \text{ (SE: } 2.59).$$

Production of adults by the hatchery is estimated to be 5 to 6 times that of natural production, although the precision of that estimate is extremely low, as indicated by the standard error–a rough 95% confidence interval would include the possibility that survival from potential egg deposition to adult was smaller for hatchery operations than for natural spawning.

Survival from Marking Effects

Estimates of the initial numbers of unmarked creek and hatchery fry are 68,400 and 495,000, respectively. Unmarked recoveries to the weir totaled 5,545. Survival of marked fry to return at the weir is estimated by the ratios of marked recoveries at the weir (Table 2) to numbers of marked fry released, or 71/5,500 = 0.01291 for creek fry and 644/84,000 = 0.00767 for hatchery fry. Then survival from marking is estimated to be

$$[(68{,}400)(0.01291) + (495{,}000)(0.00767)]/5{,}545 = 0.84.$$

Determination of the precision of the marking mortality estimate was not attempted because of the apparent complexity of the problem.

Fry Size and Developmental Index

Most of the fry from gravel incubators were shorter (Figure 4) but heavier (Figure 5) than creek fry, although there were two exceptions: fry from incubator A had an average weight of 260.0 mg, which was not significantly different from the average weight for creek fry–260.2 mg (Table 3);

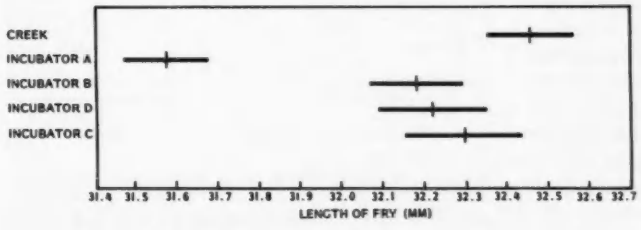

FIGURE 4.–Weighted means and 95% confidence intervals for these means of lengths of preserved fry from Auke Creek and four gravel incubators.

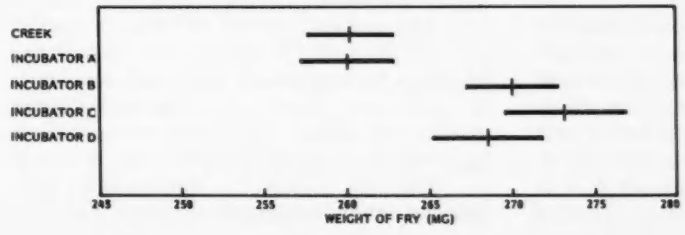

FIGURE 5.–Weighted means and 95% confidence intervals for these means of weights of preserved fry from Auke Creek and four gravel incubators.

TABLE 3.—Pooled means and variances of means for lengths, weights, and development index, K_D, of pink salmon fry (50 fry/sample) at Auke Creek in spring of 1973.

Source	Number of samples	Length (mm)		Weight (mg)		K_D index	
		Mean	Variance	Mean	Variance	Mean	Variance
Creek	13	32.45	0.00272	260.2	1.630	1.964	5.36×10^{-5}
Incubator:							
A	8	31.57	0.00252	260.0	1.917	2.008	5.50×10^{-5}
B	8	32.17	0.00276	269.9	1.856	2.009	5.54×10^{-5}
C	4	32.21	0.00412	273.2	3.352	2.012	9.61×10^{-5}
D	5	32.29	0.00483	268.6	2.714	1.987	9.92×10^{-5}

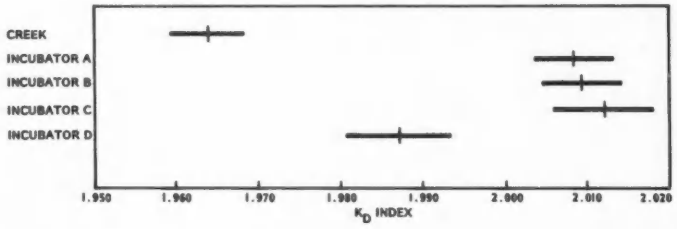

FIGURE 6.—Weighted means and 95% confidence intervals of these means of indices of development, K_D, of preserved fry from Auke Creek and four gravel incubators.

and fry from incubator D had an average length of 32.29 mm, which was not significantly different from the average length for creek fry—32.45 mm.

Indices of development were higher for fry from all the gravel incubators than for creek fry (Figure 6). The mean indices of development for gravel incubator fry ranged from 1.987 to 2.012, whereas the mean for creek fry was only 1.964 (Table 3). In an earlier test (Bailey and Taylor 1974) the average K_D index decreased about 0.005 unit/day in the final stages of alevin development. Since the average K_D index for incubator fry was 0.016 unit higher than the index for creek fry, incubator fry apparently emerged about 3 days earlier in their development.

Time of Emergence and Seaward Migration

Fry of the 1972 brood from the gravel incubators migrated voluntarily between 15 March and 23 May 1973; the median date was 14 April (Figure 7). Creek fry emigrated between 16 March and 15 May; the median date was 27 April (Figure 7).

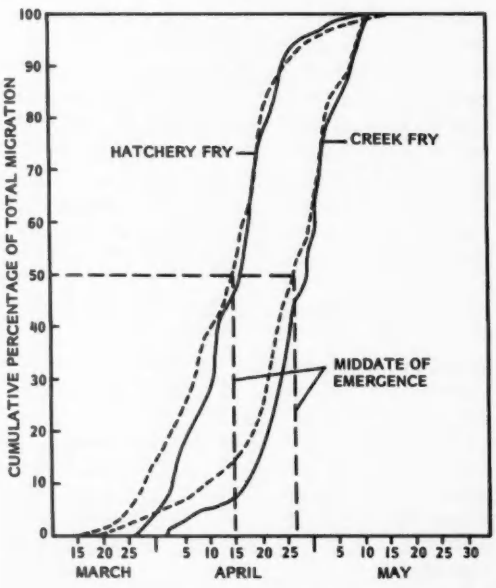

FIGURE 7.—Daily cumulative percentage of pink salmon fry migrations of creek fry and hatchery fry from Auke Creek in 1973; solid lines represent fin-marked fry and dashed lines represent total fry in the respective migrations.

Size of Returning Adults

Length measurements of adults from the 1972 brood that returned to the weir in 1974 are classified by sex, origin (whether creek or hatchery), and time of return (either early or late run). Mean lengths and sample sizes (Table 4) were used as basic observations with which to perform an analysis of variance (Scheffé 1959: 362-363) to search for differences in size among the classifications. Analyses were performed separately for each sex because underlying variances of hatchery fish differed significantly between sexes. Spawning males typically vary more in length than spawning females. The corresponding tests for creek fish did not indicate inequality of vari-

TABLE 4.–Average lengths of adult pink salmon returning to Auke Creek weir, early and late runs; the figures in parentheses represent the number of fish in the samples.

		Average lengths (mm)			
		Early run		Late run	
Mark	Origin	Male	Female	Male	Female
Unmarked	Hatchery and creek	493.1 (117)	495.2 (92)	512.4 (58)	500.8 (137)
Ad-LV[1]	Hatchery	500.2 (126)	499.6 (70)	510.0 (44)	495.6 (44)
Ad-RV[2]	Creek	505.6 (19)	515.9 (7)	515.7 (3)	497.3 (3)

[1]Ad-LV = adipose and left ventral fins.
[2]Ad-RV = adipose and right ventral fins.

ances, probably because of the small sample sizes.

Differences in length due to origin, time of return, or interaction were not detectable at the 95% level of testing for either sex (Table 5). Only time of return for females approached statistical significance (the test would have been significant at the 90% level). Mean lengths of samples of creek fish exceeded those of hatchery fish in all cases (Table 4). While our data suggest that creek fish were larger than hatchery fish upon return, the observed differences could be due to chance when samples were drawn. Larger samples would have been needed to resolve the issue.

TABLE 5.–Analysis of variance of size of returning adult male and female pink salmon classified by origin (creek or hatchery) and time of return (early or late).

Source	Degrees of freedom	Mean square	F
Males:			
Origin, A	1	30.8025	<1
Timing, B	1	99.0025	<1
AB	1	0.0225	<1
Error	188	161.543	—
Females:			
Origin, A	1	81.000	2.09
Timing, B	1	127.690	3.30
AB	1	53.290	1.38
Error	120	38.739	—

Timing of Adult Return

Marked hatchery fish entered the weir between 6 August and 25 September and marked creek fish entered between 16 August and 20 September (Figure 8). For 644 marked hatchery fish the median date of return was 13 September 1974; for 71 marked creek fish the median date was 10 September.

DISCUSSION

Gravel incubation of eggs and release of unfed fry increased the survival from potential egg deposition to returning adult an estimated 5 to 6 times over natural spawning for 1972 brood year pink salmon at Auke Creek. The estimate lacks precision, however, and a rough 95% confidence statement includes the possibility that egg-to-returning-adult survival was less for incubator fry than for naturally produced fry. Further, the estimate of relative survival is potentially biased unless marine mortality due to marking and fishing was similar for both groups of marked fry. The similarity of timing of adult returns from both groups gives no reason to suspect differential fishing mortality. The low mortality of creek fry in the fyke net and live-box suggests only slightly greater physical abuse occurred to marked creek fry than hatchery fry. The difference in survival from potential egg deposition to returning adult, if real, was accomplished in spite of certain deficiences in the quality of environment provided for eggs and alevins in the hatchery and in spite of

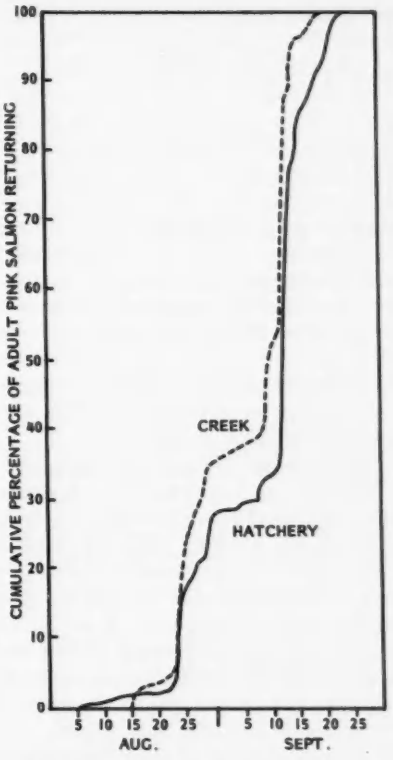

FIGURE 8.–Daily cumulative percentage recovery of marked adult pink salmon at Auke Creek weir, 1974.

a lower ocean survival for hatchery fry than for creek fry.

There is a notable difference in survival from marking in the tests at Auke Creek and the tests by Bams (1972, 1974) at Headquarters Creek, Vancouver Island. The estimate of survival from marking at Auke Creek, 84%, is much greater than the 17% and 36% survival we estimated from Bams' data on Headquarters Creek. Intertidal alevin production in Auke Creek below the weir was estimated by hydraulic pump survey to be 16% of that above the weir. Possible straying of these intertidal fish above the weir upon return would only bias our estimate below actual survival from marking. The slower rate at which our technicians clipped fins may be the cause of better survival from marking at Auke Creek.

Our estimates of fry releases and survivals imply that an increase in numbers of returning spawners at Auke Creek in 1974 was largely due to operation of the hatchery. If this is true, then hatcheries can be built on lake-water sources with a reasonable expectation of successfully enhancing salmon numbers. Projections of our data must be considered tentative because of the lack of precision. However, the magnitude of the Auke Creek escapement in relation to escapements to other streams in northern southeastern Alaska supports our conclusion that operation of the Auke Creek Hatchery did in fact enhance the return of adult salmon. For example, marked hatchery fry had a recovery rate of 0.767%. Survival from marking was 84%. The release of 579,000 hatchery fry would project to (579,000)(0.00767)/0.84 = 5,287 adults. The projected return of creek fry would be (84,000)(0.01291)/0.84 = 1,291 adults. In 1974, 6,260 adults returned to the Auke Creek weir from a parent escapement of 1,768 adults. This 3.5-fold increase occurred in the face of a general scarcity of pink salmon in this part of Alaska. According to Kingsbury (1975) the lowest escapement for pink salmon streams of northern southeastern Alaska since 1960 occurred in 1974.

The yolk content of fry when they leave the incubating bed, either natural or artificial, bears directly on the survival of the fry in the wild. Fry with a large amount of yolk have not attained their maximum potential size, are relatively poor swimmers, may not be able to osmoregulate in seawater, and are more vulnerable to predators. On the other hand, fry that have little or no yolk are losing weight and soon become weakened and emaciated and again are more vulnerable to predators. Naturally produced fry emerge volitionally from the stream gravel, presumably at the stage of development that ensures maximum survival. Our analysis of the developmental index showed our gravel incubator fry emerged prematurely in comparison to creek fry.

Earlier (in the temporal sense) emergence of fry produced in gravel incubators at Auke Creek also suggests that the Auke Creek Hatchery environment was inferior to the natural streambed environment. Hatchery fry emerged and migrated seaward 2 wk earlier than creek fry. This could place them in the estuary before the spring bloom of zooplankton on which they feed and before spring warming of estuarine surface water. The resulting slow growth rate could mean an excessively long period of high vulnerability to predators. Experiments by others (Levanidov 1964; Bams 1967; Kanid'yev et al. 1970; Parker 1971) show that small juvenile salmon suffer higher mortality from predation than large juvenile salmon.

The earlier time of migration and size of hatchery fry at Auke Creek were probably caused by one or more of the following: the higher average winter temperature of Auke Lake water (4°C) as compared to the temperature in natural redds in Auke Creek (0°-2°C); the low oxygen content of 60-70% saturation in lake water supplied to incubators; and the brown organic material from iron bacteria which accumulated in the gravel incubators and impeded the flow of water.

ACKNOWLEDGMENTS

We thank Joyce Gnagy, biologist at the Auke Bay Fisheries Laboratory, for identifying the organic growth in the gravel incubators. We also thank personnel of the Alaska Department of Fish and Game who reported the recovery of marked fish in the sport and commercial fisheries.

LITERATURE CITED

BAILEY, J. E., AND S. G. TAYLOR.
1974. Salmon fry production in a gravel incubator hatchery, Auke Creek, Alaska, 1971-72. U.S. Dep. Commer., NOAA Tech. Memo. NMFS ABFL-3, 13 p.

BAMS, R. A.
1967. Differences in performance of naturally and artificially propagated sockeye salmon migrant fry, as measured with swimming and predation tests. J. Fish. Res. Board Can. 24:1117-1153.

1970. Evaluation of a revised hatchery method tested on pink and chum salmon fry. J. Fish. Res. Board Can. 27:1429-1452.

1972. A quantitative evaluation of survival to the adult stage and other characteristics of pink salmon (*Oncorhynchus gorbuscha*) produced by a revised hatchery method which simulates optimal natural conditions. J. Fish. Res. Board Can. 29:1151-1167.

1974. Gravel incubators: a second evaluation on pink salmon, *Oncorhynchus gorbuscha*, including adult returns. J. Fish. Res. Board Can. 31:1379-1385.

BURROWS, R. E.

1951. Method for enumeration of salmon and trout eggs by displacement. Prog. Fish-Cult. 13:25-30.

DEMING, W. E.

1943. Statistical adjustment of data. John Wiley & Sons, Inc., N.Y., 261 p.

KANID'YEV, A. N., G. M. KOSTYUNIN, AND S. A. SALMIN.

1970. Hatchery propagation of the pink and chum salmons as a means of increasing the salmon stocks of Sakhalin. J. Ichthyol. 10:249-259.

KASAHARA, H.

1963. Catch statistics for North Pacific salmon. Int. North Pac. Fish. Comm., Bull. 12:7-82.

KINGSBURY, A. P.

1975. Salmon strategy, tight management for southeastern pinks. Alaska Fish Tales and Game Trails 9(6):1, 14-15.

LEVANIDOV, V. YA.

1964. O zavisimosti mezhdu razmerami mal'kov Amurskoi osennei kety *Oncorhynchus keta* infrasp. *autumnalis* Berg i ikh vyzhivaemost'yu. Vopr. Ikhtiol. 4:658-663.

MCNEIL, W. J.

1964. A method of measuring mortality of pink salmon eggs and larvae. U.S. Fish Wildl. Serv., Fish. Bull. 63:575-588.

PARKER, R. R.

1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Board Can. 28:1503-1510.

PAULIK, G. J., AND D. S. ROBSON.

1969. Statistical calculations for change-in-ratio estimators of population parameters. J. Wildl. Manage. 33:1-27.

SCHEFFÉ, H.

1959. The analysis of variance. John Wiley & Sons, Inc., N.Y., 477 p.

SEIBEL, M. C., AND C. P. MEACHAM (editors).

1975. A summary of preliminary 1975 forecasts for Alaskan salmon fisheries. Alaska Dep. Fish Game, Inform. Leafl. 167, 55 p.

SNEDECOR, G. W.

1956. Statistical methods applied to experiments in agriculture and biology. 5th ed. Iowa State Coll. Press, Ames, 534 p.

COMPARISON OF THE MOST SUCCESSFUL AND LEAST SUCCESSFUL WEST COAST ALBACORE TROLL FISHERMEN

DONALD F. KEENE[1] AND WILLIAM G. PEARCY[2]

ABSTRACT

Catch data for albacore troll boats were collected from fishermen's logbooks and from dockside interviews during the 1968, 1969, and 1970 seasons. Fishing powers of these boats were calculated and used to determine the 10 most successful and 10 least successful fishermen (highliners and lowliners, respectively) who fished off Oregon and Washington. Characteristics of these two groups of fishermen were then compared. In general, highliners had longer boats and fished nearer the fleet center and along the offshore margin of the fleet. Lowliners tended to have smaller boats and fished along the trailing (south) inshore margin of the fleet. Both groups responded to changes in apparent albacore abundance by aggregating on days of high apparent abundance, although this response was less pronounced in 1969 and 1970. Highliners caught significantly smaller (but more) fish than the lowliners.

The west coast albacore troll-boat fleet consists of many types and sizes of vessels (Clemens 1955). Troll boats range in length from about 10.7 m (35 feet) to over 22.9 m (75 feet) with a displacement of about 15 tons. Part of this fleet begins fishing for albacore off the coast of Baja California in early summer. During the peak of the season (July, August, September) boats may be found from Mexico to the Gulf of Alaska. However, the most productive area usually lies between central Baja California and the Columbia River (Clemens 1961). Many boats, particularly those from Oregon and Washington, fish for other species (salmon, crab, shrimp) during part of the year (Roberts 1972) and occasionally during the albacore season when albacore fishing is slow.

Fishermen in the albacore fleet exhibit a large range of fishing success. Fishing success has been related to strictly physical parameters of the vessel, such as boat length (Fox[3]). Abramson (1963) suggested that fishing success is related to the skill and experience of the captain and crew, as well as the physical parameters of the boat. Little is known, however, about how fishing success is related to the activities of individual albacore fisherman and the activities of the surrounding fleet. (The fleet is considered to be an assemblage of fishing boats within an area of arbitrarily chosen size.) The objective of this paper is to describe and compare the characteristics and movements of the most successful with those of the least successful albacore fishermen during the 1968, 1969, and 1970 seasons.

METHODS

Sources and Treatment of Data

Information on number of fish caught per day by troll boats, location of the catch, boat length, and number of lines (1970 only) was collected from three sources for the 1968, 1969, and 1970 albacore seasons: 1) logbooks distributed by Oregon State University (1969 and 1970), 2) logbooks distributed by California Department of Fish and Game to fishermen who volunteered to submit daily information, and 3) interviews obtained by personnel of the Oregon Fish Commission at dockside during unloading of the albacore. Careful screening avoided duplication of logbook records since vessels often submitted records to more than one source. Only catch locations between lat. 42° and 49°N were used.

The number of reporting boats varied considerably between years. In 1968, 205 boats reported their daily catches and locations. In 1969 and 1970, 70 and 113 boats, respectively, reported. The total number of boats fishing during the 3 yr is unknown but is estimated to have been between 750 (Panshin 1971) and 1,000.

Data from the logbooks and interview sheets

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[3]Fox, W. W. "Fishing power of U.S. vessels participating in the Pacific coast albacore fishery 1961-1970" Paper presented at the 24th Tuna Conference, Lake Arrowhead, Calif., Oct. 1973.

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were punched on computer cards. Each card contained three pieces of information: the boat number, an area-data code (signifying the 1° latitude by 1° longitude rectangle and the calendar day), and the boat's catch of the day. There were approximately 3,300 observations in 1968, 1,500 in 1969, and 1,000 in 1970.

A particular boat was chosen to represent the standard unit of effort. Criteria for the standard boat choice included the following: it fished 1) during all three seasons; 2) in area-date strata concurrently with a majority of the fleet; 3) most of each season; and 4) consistently to provide a standard, nonvarying reference for the other boats.

Estimates of fishing power[4] of all boats in the fleet were initially determined relative to the standard boat. This was accomplished using a computer program called FPOW (Berude and Abramson 1972). FPOW utilizes Robson's (1966) linear two-factor analysis model for estimating the relative fishing power of fishing vessels. The estimates of fishing power derived from the model are logrithms. FPOW provides an approximate correction for this bias using a Taylor series expansion of the estimate about its true value. The method and assumptions used in FPOW are described in Robson (1966) and Abramson and Tomlinson (1972:1022-1023). The program's storage capacity was limited to 2,000 catch observations from a combined total of not more than 200 distinct boats and area-date strata. Data for each year were broken up into time segments short enough to satisfy this limitation. Ten segments were required in 1968, five in 1969, and three in 1970. Each segment was run independently and provided estimates of each boat's relative fishing power during the time segment.

Considerable within-season variation occurred in the average fishing power of the fleet (Table 1), suggesting that the standard boat fished inconsistently relative to the fleet. An examination of the logbooks showed that the standard boat occasionally experienced periods of very low catches (10 to 15 fish per day) while the majority of the fleet in the immediate area was catching 100 to 200 fish per boat. This was particularly obvious during segment 1 of the 1969 season.

As a result of the standard boat's inconsistent fishing, values of standardized catch per boat day were also inconsistent between data segments. For example, an average boat had fishing powers of 3.70 and 1.01 on 25 July and 26 July 1969, respectively (Table 1). If the average boat caught 100 fish on 25 July and 100 on 26 July 1969, values of standardized catch per boat day (100 fish/average fishing power) would be 27 and 99, respectively, for these 2 days. Therefore a serial examination of apparent abundance could not be performed without normalizing fishing power estimates of each boat in each data segment.

Fishing power estimates were normalized by subtracting the appropriate segment's average fishing power from each boat's fishing power and adding unity. (By definition the standard unit of effort is 1.0.) Each boat's fishing power estimate was now relative to the average fishing power of all boats fishing during the data segment. This procedure required the assumption that the fleet fished consistently relative to the standard boat throughout each season.

Daily standardized catch per boat within each area-date stratum was determined by summing the fish catches and dividing by the summation of fishing power in that area-data stratum. The standardized catch per boat day is an index of

TABLE 1.—Data segments for the 1968, 1969, and 1970 albacore seasons.

Segment	Dates	No. of obs.	No. of boats	No. of area-dates	Average fishing power
1968:					
1	6-16 July	242	60	47	0.69
2	17-21 July	320	85	34	1.14
3	21-31 July	410	74	76	0.99
4	1-4 Aug.	357	109	45	0.91
5	5-7 Aug.	290	108	33	0.70
6	8-11 Aug.	310	100	39	0.88
7	12-18 Aug.	420	88	78	0.82
8	19-24 Aug.	373	82	69	1.03
9	25-30 Aug.	235	72	46	0.53
10	31 Aug.-10 Sept.	385	70	113	0.99
1969:					
1	15-25 July	305	51	59	3.70
2	26 July-3 Aug.	374	66	60	1.01
3	4-11 Aug.	326	65	59	1.15
4	12-18 Aug.	212	56	63	1.47
5	19 Aug.-11 Sept.	296	40	111	1.16
1970:					
1	15-22 July	160	52	64	0.35
2	23-28 July	470	99	54	0.91
3	29 July-2 Sept.	262	65	86	0.67

[4]Fishing power is defined (Beverton and Holt 1957:172) as the ratio of the catch per unit of fishing time of a particular vessel to that of another vessel designated as the standard. It is assumed that both boats must have fished on the same density of fish during the same time interval and within the same fishing area when the ratio is determined. Fishing success, on the other hand, is related to fishing power but is more descriptive. It includes parameters difficult to quantify. For example, fishing success may include crew motivation, attitude, and access to useful information. Together with fishing power, these parameters are determinants of fishing success.

apparent abundance, the latter being a function of the accessibility of the albacore to the boats, the vulnerability of the fish to the lures (Marr 1951), and the true abundance of albacore.

The 10 most successful and 10 least successful fishermen (highliners and lowliners, respectively) of each season were selected according to their boats' average fishing power estimates throughout the entire season. Highliners and lowliners selected had fished for at least 15 days in 1968 and 1969 and 8 days in 1970. Thus fishermen who fished exceptionally well or poorly for only a few days in a season were not considered.

Area-Date Stratum of Apparent Abundance

Small-scale time and space information of catches and boat positions allowed a departure from the traditional time-area stratum of 1 mo and 1° latitude-longitude rectangle (Ayers and Meehan 1963; Clemens and Craig 1965). A mobile stratum was conceived to allow comparisons of apparent abundance and effort regardless of where the fleet moved, and without the problems of fixed geographic boundaries.

The new stratum was a circular area, the center being the daily medial location of the fleet. This medial point was determined such that the fleet was equally divided in the north-south and east-west planes. Criteria for the radius of the circular area were that it should be 1) as small as possible to include a homogeneous distribution of fish, but 2) large enough to accommodate a sufficient number of boats fishing on a given day so that catch and effort could be reliably estimated, and 3) large enough to give reasonable assurance that boats within the area remained in the area the entire day. Because of the lack of knowledge of small-scale albacore distributions, there was little basis for satisfying the first criterion.

Consecutively larger concentric circles were drawn around the medial point while noting the ratio of boats within each circle to the number of boats in the entire fleet. (Danils (1952) has presented theoretical considerations of sample point distributions within such circles.) During much of each season, over half the boats could be found within 25 miles of the fleet's center. Exceptions occurred in each season when the fleet was highly dispersed or split into two distinct groups. Two distinct groups of boats occurred on 2, 3, and 4 August 1968 and also 1, 2, and 8 August 1969. During these days the northernmost center was chosen to represent the fleet center because it always contained more boats.

The third criterion suggested a radius of at least 31 miles to insure that vessels remained within the area the entire day. This radius was determined on the basis of distances traveled daily by albacore boats. (This is reported later in this study.) A circle with a radius of 31 miles was therefore used as the area size. Figure 1 shows the percentage of boats that provided catch data within 31 miles of the fleet center each day during the 1968, 1969, and 1970 seasons. Only the time periods within the vertical lines in Figure 1 will be considered for this study. On days outside these periods few boats reported their catch, or the fleet was small and highly dispersed. The average daily percentage of those boats reporting within 31 miles of the fleet center was 46%, 57%, and 65% for the 1968, 1969, and 1970 seasons, respectively. The differences between the 1968 average and the 1969 and 1970 averages were highly significant (t-test, $P<0.01$), indicating that the 1968 fleet was more dispersed in general than the 1969 and 1970 fleets. (This was not a result of a greater number of boats reporting in 1968 because the number of boats reporting per day was often greater in 1969 and 1970 than in 1968.) There was a tendency in both 1968 and 1969

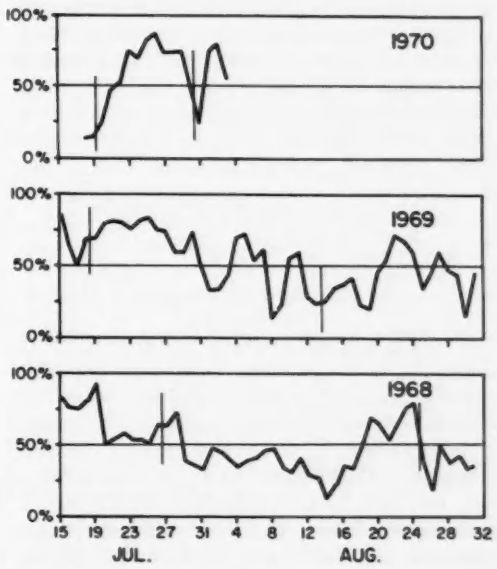

FIGURE 1.—Daily percentage of boats within 31 miles of the albacore fleet center; 1968, 1969, and 1970. Vertical lines on plots indicate the time periods considered in detail in this study.

for the fleet to become more dispersed as the season progressed.

Aggregation of the Boats

The index of aggregation used in this study was the mean separation distance of boats within a specified area. The index was determined by summing separation distances between all boats in the area and dividing this sum by the number of separation distances. This calculation required converting LORAN coordinates (given as the 2100 h PDT boat positions) to latitude-longitude coordinates. Accuracy of the iterative technique used to compute the coordinates has been estimated at 10 m (Thomas 1965:7-9, 38-52), although the absolute position accuracy varied considerably due to the precision of the LORAN operator and the distance from the LORAN transmitters. Boat positions reported at 2100 h within 200 miles of the coast are estimated to be within 3 miles of the absolute positions.

Hunter (1966) stated that mean separation distance is preferred for measuring relative changes in spacing, but for comparison of samples containing different numbers of individuals, mean distance to nearest neighbor (Clark and Evans 1954) should be used. We did not use mean distance to nearest neighbor because most fishermen fish together with one or more companion boats. Mean distance to nearest neighbor would thus represent the average distance separating the same groups of boats and would give little if any information on actual compactness of the fleet within a specified area.

RESULTS AND DISCUSSION

Fishing Power Versus Boat Length and Number of Lines

Sixty-six area-date strata (1° latitude by 1° longitude rectangles and 1-day periods) were selected to examine the relationship between the fishing power of a boat and its length and number of lines trolled. All strata had at least 20 boats reporting within them. (The new mobile stratum was not used here because the intent was to partition the fishery area into a number of equal quadrats, the size and location of the quadrat being of no consequence. Daily boat positions had been assigned to 1° longitude rectangles by FPOW, so this stratum was used for convenience.)

Fishing power estimates were then regressed on boat length and number of lines. (Data on number of lines were available only for the 1970 season.) In none of the strata, in any season, was a significant regression (F-test, $P < 0.05$) found. This indicated that no significant relationship existed between a vessel's fishing power and its length or reported number of lines trolled within a given 1° by 1° rectangle during any given day.

Because of the scatter of data for small-scale time and area strata, the above conclusion did not rule out the possibility of a significant relationship between fishing power and boat length or number of lines. Therefore, a larger stratum was chosen which included all data for each year. Fishing power estimates were again regressed on boat length (1968, 1969, 1970) and number of lines (1970). The results are shown in Table 2.

Boat length was significantly related ($P<0.05$) to fishing power of albacore boats in a time-area stratum of one season and the entire fishery, particularly in 1968. The significance of boat

TABLE 2.—Regression equations and analysis of variance data for boat length (in meters) and number of lines (1970) versus boat fishing power.

1968 — Fishing power = 0.238 + 0.046 (boat length)
FP (12.2-m boat) = 0.798
FP (18.3-m boat) = 1.078

Source	df	Sum of squares	Mean square	F value
Total	810	185.459	0.229	
Regression	1	13.835	13.835	
Residual	809	171.624	0.212	65.23**

1969 — Fishing power = 0.263 + 0.049 (boat length)
FP (12.2-m boat) = 0.863
FP (18.3-m boat) = 1.163

Source	df	Sum of squares	Mean square	F value
Total	271	165.265	0.610	
Regression	1	3.214	3.214	
Residual	270	162.051	0.600	5.35*

1970 — Fishing power = 0.636 + 0.022 (boat length)
FP (12.2-m boat) = 0.916
FP (18.3-m boat) = 1.056

Source	df	Sum of squares	Mean square	F value
Total	200	24.777	0.129	
Regression	1	0.698	0.698	
Residual	199	24.079	0.121	5.76*

Fishing power = 0.816 + 0.018 (number of lines)
FP (8 lines) = 0.960
FP (12 lines) = 1.032

Source	df	Sum of squares	Mean square	F value
Total	200	24.777	0.139	
Regression	1	0.110	0.110	
Residual	199	24.667	0.124	0.89 ns

** significant at the 0.01 level.
* significant at the 0.05 level.
ns nonsignificant.

length as it related to fishing power was considerably less in 1969 and 1970 than in 1968, although the 1968 and 1969 regression equations were nearly identical.

Fox (see footnote 3) reported that fishing power of albacore troll boats was related to boat length in a curvilinear manner for the 1961-70 period, with boats of the length class 12.2 to 14.9 m exhibiting the highest estimates of fishing power. There was no clear indication of a curvilinear relationship in 1968, 1969, or 1970, although several very long boats (>22.9 m) generally did not have as large fishing powers as the linear relationship predicted, thus supporting Fox's conclusions. The sample of boats used by Fox was considerably larger (10 yr) and therefore had many more observations of longer boats than used in this study.

Large boats, moreover, make up a minor portion of the albacore fleet. The average length (and standard deviation) of the sample of boats in 1968, 1969, and 1970 was 14.9 m (2.7), 14.9 m (2.1), and 15.2 m (2.7), respectively. Some fishermen feel that larger boats are more successful because of their increased seaworthiness and endurance, resulting in fewer trips to port and permitting more time on the fishing grounds. Fishermen also feel that larger boats fish the lures better in rough weather. Whereas smaller boats tend to jerk the lures as the waves hit the boats, larger boats push smoothly through the waves with less jerking of the lures.

The reported number of lines trolled in 1970 was not significantly related to fishing power. The number of lines reported varied from 6 to 14, with 10 being the mean and mode. The standard deviation was 1.0. The number of trolling lines reported on log sheets bears little resemblance to the number of lines used during varying periods of fishing activity, according to fishermen. When fishing activity increases, only two or possibly three lines are pulled by each man. During periods of intense activity, each man may only handle one line, although periods of intense activity are usually of very limited duration. When the catch rate increases, the longest lines are pulled on board first and only the short lines are fished. One fisherman stated that the number of lines used was determined primarily by the ability of the crew in avoiding tangling of lines. However, over 90% of the 1968 logbooks (in which crew size was recorded) indicated a crew size of two. It would appear that the possible increase in catch as a result of a larger crew size during the infrequent periods of intense fishing activity are offset by the increase in financial cost of a larger crew size. This is even more apparent considering that a daily catch of 180 fish (i.e., about 5 fish per hour per man for a two-man crew) is considered a very good catch by an albacore fisherman.

Comparison of Highliners and Lowliners

Some comparisons of highliner and lowliner boats are given in Table 3. Both groups fished approximately the same number of days and in the same period each season. The difference in boat length was highly significant in all years, particularly in 1968 when highliner boats averaged 4.9 m longer than lowliner boats. In 1969 and 1970 only 1.5 m separated the average length of highliner and lowliner boats. Seven of the 1968 highliner boats were over 15.5 m, whereas none of the 1969 and only one of the 1970 highliner boats were over 15.5 m. Essentially the same proportions of 15.5 m and longer boats made up the fleet samples in each season. Lowliner boat lengths were consistently short, between 14.0 and 15.2 m.

Lowliners often fished along the trailing margin of the fleet during all years as the fleet moved to the north. Highliners were more centrally located in the fleet and along the offshore or leading margin, as shown in Table 3. In 1968 lowliners were removed from the main body of the fleet, generally located far to the south and inshore of the fleet, whereas highliners tended to be slightly to the south but offshore of the main fleet center. In 1969 and 1970 both groups were located closer to the fleet center, although the lowliners were still three to four times farther away from the fleet center than were highliners. Lowliners fished consistently south of the center in all 3 yr.

A detailed description of the location of highliners and lowliners is presented in Figures 2-4.

TABLE 3.—Comparison of highliners with lowliners, west coast albacore trollers.

Item	1968	1969	1970
Average boat length (m):			
Highliners	19.2	15.5	16.2
Lowliners	14.3**	14.0**	14.6**
Average distance to fleet center (miles):			
Highliners	30 SW	5 W	8 N
Lowliners	104 SSE	22 SW	25 S
Average daily travel (miles):			
Highliners	21	28	27
Lowliners	31**	29 ns	28 ns
Average relative fishing power:			
Highliners	1.61	1.57	1.24
Lowliners	0.65	0.46	0.85

** significant at the 0.01 level, *t*-test.
ns nonsignificant.

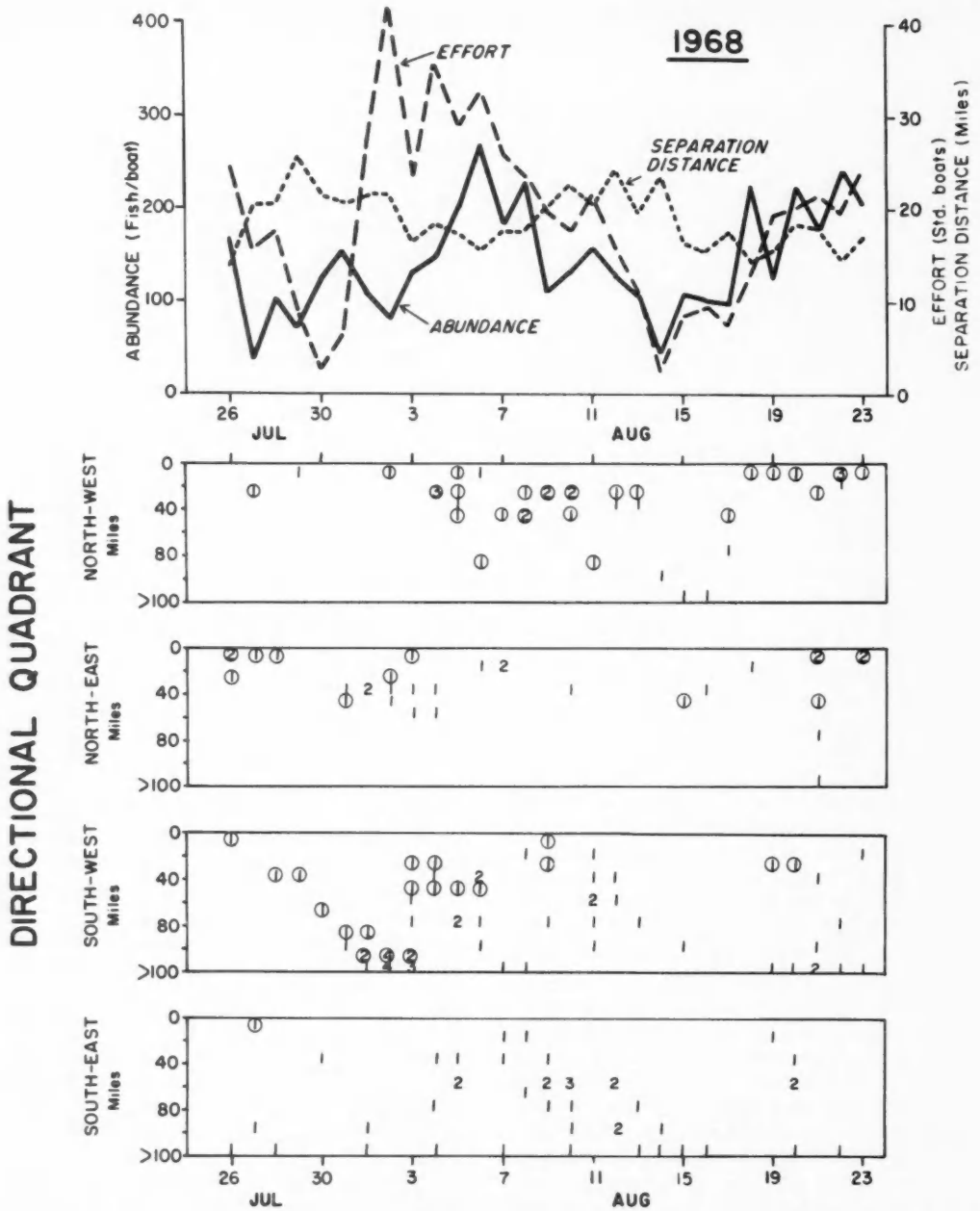

FIGURE 2.–Locations of 1968 highliners and lowliners relative to the center (medial) of the fleet. The top graph indicates the corresponding levels of apparent abundance of albacore, fishing effort, and boat separation distance within 31 miles of the fleet center. The lower four plots show the distance of highliners (circled numbers) and lowliners (noncircled numbers) from the medial fleet center.

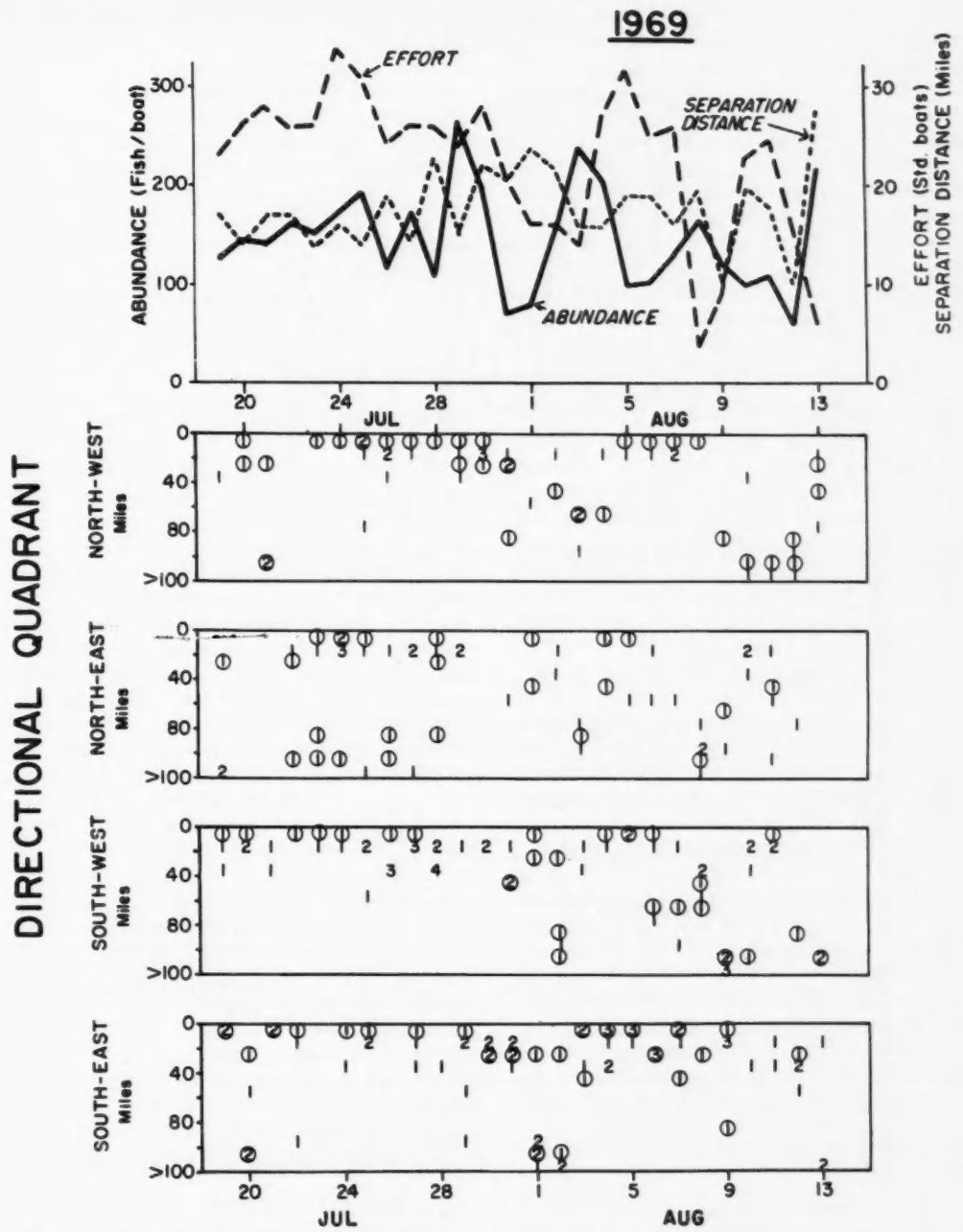

FIGURE 3.–Locations of 1969 highliners and lowliners relative to the center (medial) of the albacore fleet. See Figure 2 for explanation of plots.

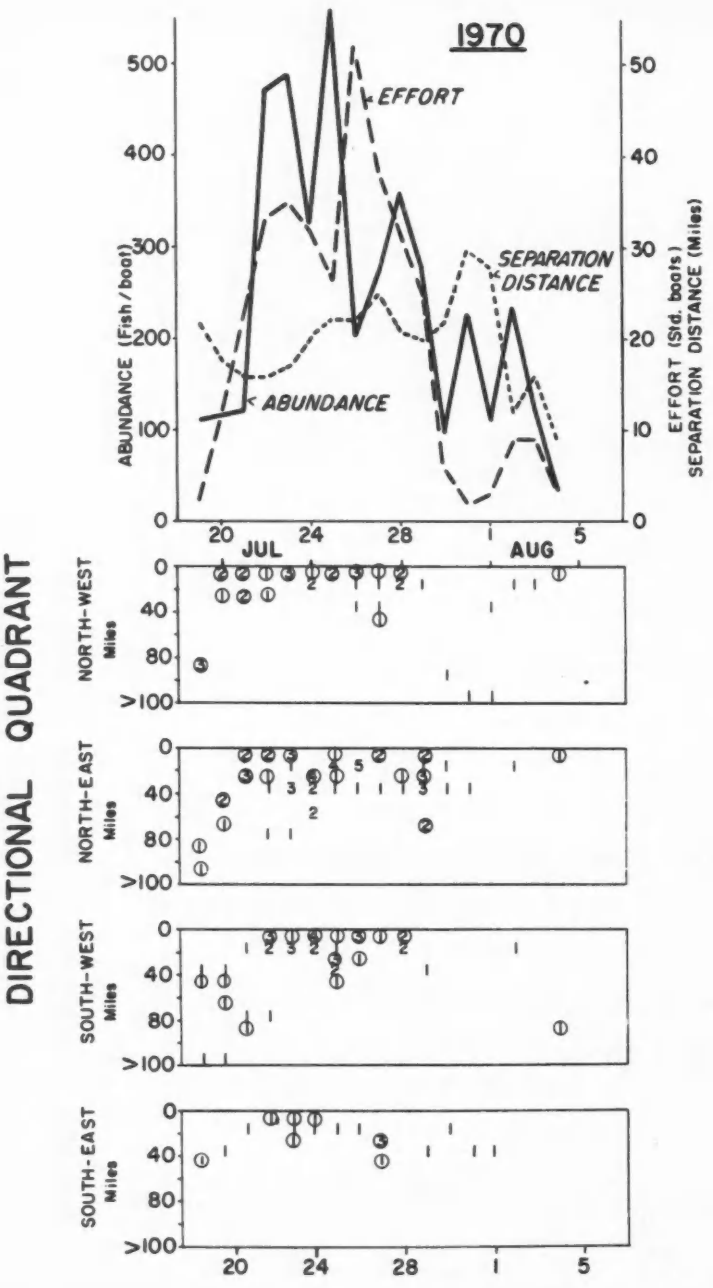

FIGURE 4.—Locations of 1970 highliners and lowliners relative to the center (medial) of the albacore fleet. See Figure 2 for explanation of plots.

The plots show where these two groups fished with respect to the fleet center during periods of variable levels of albacore abundance, fishing effort, and boat separation distance (shown at the top of the figures).

A very obvious separation of highliners and

lowliners occurred in 1968 (Figure 2). Highliners fished almost exclusively to the northwest and southwest of the fleet center. When abundance was low and effort high (26 July-3 August), highliners moved far from the fleet center, as seen in the southwest quadrant. During 5 and 6 August, when high catches coincided with high levels of effort, highliners were found close to the fleet center, but not as close as during periods of low effort. Lowliners fished mainly to the south and away from the fleet center during all levels of abundance. When abundance was high (5-8 August), lowliners in the southeast quadrant moved closer to the fleet center. Later as catches declined, the lowliners moved away from the center (southeast quadrant, 9-15 August).

There was no obvious separation of highliners and lowliners in 1969 (Figure 3) comparable to 1968. Highliners fished in all quadrants, as did lowliners. Some highliners fished away from the fleet center during periods of low abundance (31 July-2 August; 5-12 August), particularly in the northwest and southwest quadrants when effort was high (10-12 August). Lowliners again fished more in the southern quadrants than did highliners but not exclusively so and not as far from the fleet center as in 1968. In fact, most lowliners were located near the fleet center until all catches began decreasing after 5 August. Then, some lowliners moved away from the fleet (southwest, northeast; 10-11 August) but the majority remained near the fleet center.

The short 1970 season provided little information on the responses of highliners and lowliners (Figure 4). As the season began (19-21 July) highliners were fishing at some distance from the fleet center. During the period of very high catches (22-29 July) both highliners and lowliners fished within 40 miles of the fleet center. No boat reported a location farther than 80 miles from the center during this time. There was no indication that either group dispersed in response to the high levels of effort and aggregation of boats which occurred. On 22 July, when separation distance was lowest and on 26 July when effort was highest, most highliners were fishing within 20 miles of the fleet center.

Most highliners did not fish Oregon waters after 30 July, the day catches dropped precipitously. The lowliners that stayed were northwest of the fleet center. Catches never returned to their original high levels, and on 4 August the season was essentially over for the troll boats.

Some albacore fishermen believe that large numbers of small fish are located in the offshore fishing area and that highliners are able to exploit these fish to a greater degree because of their greater endurance and seaworthiness. To test this hypothesis, the average weight of each fish per trip reported by highliners during July and August was compared with the average fish weight per trip for lowliners. The results, given in Table 4, show that highliners caught significantly smaller fish than lowliners. This supports the fishermen's belief that smaller fish are found along the offshore margins of the fishery where highliners often fish, while larger fish are found along the inshore margins of the fishery where lowliners expend more effort.

The difference between average daily net travel of highliners and lowliners, based on 2100 h PDT positions, changed significantly within the 3 yr. Highliners in 1968 moved 10 miles less per day than did lowliners (Table 3). In 1969 and 1970 there was no statistical difference between the average distance traveled by the two groups. Travel distances in Table 3 can be compared with the daily travel of the fleet center (Figure 5). The fleet center moved an average of 14 miles per day in 1968, 29 miles per day in 1969, and 29 miles per day in 1970. Highliners moved in a much closer relationship with the fleet in 1968 than did lowliners. Lowliners in 1968 traveled twice as far as the general fleet, yet lagged behind the fleet's northerly movement. This was much less apparent in 1969 and 1970.

A comparison of average relative fishing powers showed that highliners of 1968 and 1969 were about three times more successful than lowliners in catching fish (Table 3). Lowliner fishing power decreased in 1969, even though lowliner and highliner boat lengths and daily distances traveled were similar. In 1970 lowliner and highliner characteristics were quite simlar to those of 1969, except for calculated fishing power. In 1970 fishing power of lowliners increased while that of highliners decreased. This was probably due to the

TABLE 4.—Average weight (kilograms) of individual albacore per trip taken by highliners and lowliners during July and August 1968, 1969, and 1970.

Year	Highliners	Lowliners
1968	5.7	6.2*
1969	6.0	6.4**
1970	6.1	6.8*

* significant at the 0.05 level.
** significant at the 0.01 level.

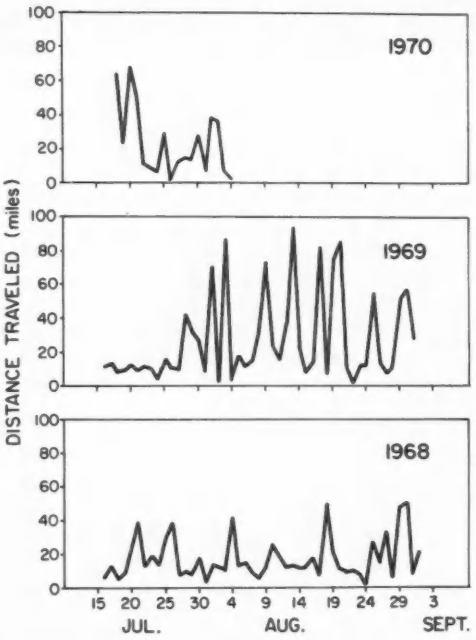

FIGURE 5.—Net daily movement of albacore fleet centers—1968, 1969, and 1970.

extremely short season on highly vulnerable fish, a situation which did not provide highliners the opportunity to utilize their capabilities and fully develop their tactics and strategies.

This study has shown that the most successful and least successful fishermen can be characterized by their activities as well as by the physical parameters of their vessels. Success is not assured by many years of experience, or by a large vessel, although these characteristics are often associated with the most successful fishermen. We agree with Abramson's (1963) suggestion that the fishing power of individual albacore boats is related to intrinsic factors of the captain and crew, in addition to the boat's physical parameters.

ACKNOWLEDGMENTS

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LITERATURE CITED

ABRAMSON, N. J.
1963. A method for computing estimates and variances of relative log fishing powers of California albacore vessels. *In* H. Rosa, Jr. (editor), Proceedings of the World Scientific Meeting on the Biology of Tunas and Related Species, p. 1209-1215. FAO Fish. Rep. 6.

ABRAMSON, N. J., AND P. K. TOMLINSON.
1972. An application of yield models to a California ocean shrimp population. Fish. Bull., U.S. 70:1021-1041.

AYERS, R. J., AND J. M. MEEHAN.
1963. Catch locality, fishing effort, and length frequency data for albacore tuna landed in Oregon, 1951-60. Oreg. Fish. Comm., Invest. Rep. 2, 180 p.

BERUDE, C. L., AND N. J. ABRAMSON.
1972. Relative fishing power, CDC 6600, FORTRAN IV. Trans. Am. Fish. Soc. 101:133.

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish, Food (G.B.), Ser. II, 19, 533 p.

CLARK, P. J., AND F. C. EVANS.
1954. Distance to neighbor as a measure of spatial relationships in populations. Ecology 35:445-453.

CLEMENS, H. B.
1955. Catch localities for Pacific albacore (*Thunnus germo*) landed in California, 1951 through 1953. Calif. Dep. Fish Game, Fish Bull. 100, 28 p.
1961. The migration, age, and growth of Pacific albacore (*Thunnus germo*), 1951-1958. Calif. Dep. Fish Game, Fish Bull. 155, 128 p.

CLEMENS, H. B., AND W. L. CRAIG.
1965. An analysis of California's albacore fishery. Calif. Dep. Fish Game, Fish Bull. 128, 301 p.

DANIELS, H. E.
1952. The covering circle of a sample from a circular normal distribution. Biometrika 39:137-143.

HUNTER, J. R.
1966. Procedure for analysis of schooling behavior. J. Fish. Res. Board Can. 23:547-562.

MARR, J. C.
1951. On the use of the terms *abundance*, *availability* and *apparent abundance* in fishery biology. Copeia 1951:163-169.

PANSHIN, D. A.
1971. Albacore tuna catches in the northeast Pacific during summer 1969 as related to selected ocean conditions. Ph.D. Thesis., Oregon State Univ., Corvallis, 110 p.

ROBERTS, K.
1972. Diversity – characteristic of Oregon's year 'round fishery. Oreg. State Univ. Sea Grant, Ext. Mar. Advis. Program 15, 2 p.

ROBSON, D. S.
1966. Estimation of the relative fishing power of individual ships. Int. Comm. Northwest Atl. Fish., Res. Bull. 3:5-14.

THOMAS, P. D.
1965. Mathematical models for navigational systems. U.S. Nav. Oceanog. Off. Tech. Rep. TR-182, 151 p.

NOTES

SEASONAL SPAWNING CYCLES OF THE SCIAENID FISHES *GENYONEMUS LINEATUS* AND *SERIPHUS POLITUS*

The white croaker, *Genyonemus lineatus* (Ayres), and queenfish, *Seriphus politus* Ayres, are two of the common inshore fishes occurring along the southern California coast (Miller and Lea 1972). Detailed reproductive data are not available for these species. The purpose of this note is to provide information on their seasonal spawning cycles.

Materials and Methods

Monthly samples are from November 1974 to October 1975. Most specimens were collected by hook and line from the Santa Monica Pier, Los Angeles County, Calif. Remaining fishes were obtained about 4.2 km south of Santa Monica at the Scattergood Steam Plant, El Segundo, Los Angeles County. Scattergood fishes had been exposed to temperatures between 23° and 41°C. Histological comparisons of these fishes with freshly caught specimens showed the ovaries were not altered by this treatment. Specimens are deposited in the ichthyology collection of the Los Angeles County Museum of Natural History.

Fishes were immediately slit and placed in 10% Formalin.[1] Gonads were embedded in paraffin and histological sections cut at 8 μm. Slides were stained using iron hematoxylin followed by eosin counterstain. Seasonal occurrences of oocytes (Tables 1, 2) were calculated by randomly selecting areas of slides from each monthly representative and classifying oocytes as to their category (Type 1, 2, or 3). Areas of a slide were surveyed until at least 100 oocytes were classified.

Results and Discussion

Three classes of oocytes are present in the ovaries of *G. lineatus* (Table 1) and *S. politus* (Table 2). Type 1 is the most abundant class and varies from those recently derived from oogonia to those approaching Type 2 oocytes. Type 2 oocytes have diameters between 100 and 270 μm and differ from Type 1 oocytes in the presence of a zona pellucida and zona granulosa. Small quantities of yolk granules may be found on the periphery of larger representatives of this class. The diameter of yolk filled mature Type 3 oocytes is greater than 270 μm. The smallest fishes to contain Type 3 oocytes measured 143 mm standard length (SL) for *G. lineatus* and 148 mm SL for *S. politus*.

As shown in Tables 1 and 2 there are several differences in seasonal distribution of oocytes reflecting the spawning cycles of *G. lineatus* and *S. politus*. The major difference is in abundance of Type 3 oocytes indicating *G. lineatus* comes into spawning condition in October and spawns intermittently into April. *Seriphus politus* enters spawning condition in April and spawns into August. These data support the findings of Skogsberg (1939) who reported that *S. politus* spawns throughout summer and *G. lineatus* spawns from November through May off California.

TABLE 1.—Monthly distribution of *Genyonemus lineatus* oocytes with mean standard length (mm) ± standard error, November 1974-October 1975.

Month	*N*	Total oocytes	Type 1 (%)	Type 2 (%)	Type 3 (%)	$\overline{SL} \pm SE$
Nov.	11	1,369	60	13	27	203.3 ± 8.7
Dec.	13	1,579	65	11	24	228.8 ± 4.6
Jan.	11	1,316	60	12	28	217.3 ± 5.9
Feb.	12	1,478	64	12	24	202.1 ± 3.9
Mar.	14	1,717	69	11	20	200.7 ± 9.8
Apr.	13	1,631	77	10	13	204.2 ± 4.4
May	19	2,138	96	1	3	218.2 ± 4.7
June	10	1,251	90	5	5	218.0 ± 2.9
July	19	2,103	95	3	2	212.0 ± 4.0
Aug.	14	1,606	96	3	1	239.8 ± 3.5
Sept.	14	1,589	90	6	4	243.0 ± 3.8
Oct.	11	1,340	75	12	13	234.5 ± 6.2

TABLE 2.—Monthly distribution of *Seriphus politus* oocytes with mean standard length (mm) ± standard error, November 1974-October 1975.

Month	*N*	Total oocytes	Type 1 (%)	Type 2 (%)	Type 3 (%)	$\overline{SL} \pm SE$
Nov.	14	1,531	100	0	0	192.8 ± 2.6
Dec.	12	1,379	100	0	0	215.2 ± 4.6
Jan.	14	1,607	100	0	0	203.7 ± 2.4
Mar.	14	1,563	93	5	2	215.2 ± 5.1
Apr.	14	1,604	71	11	18	200.2 ± 5.5
May	15	1,729	77	9	14	214.6 ± 3.1
June	14	1,736	68	13	19	217.5 ± 3.9
July	14	1,864	72	8	20	225.8 ± 3.4
Aug.	14	1,536	78	9	13	202.9 ± 4.0
Sept.	14	1,499	97	2	1	212.9 ± 3.0
Oct.	14	1,574	98	0	2	207.6 ± 3.4

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

In both species oocyte maturation is a continuous process that occurs throughout the reproductive period (Tables 1, 2) with multiple spawnings occurring. Depleted ovaries containing mainly Type 1 oocytes were not observed until conclusion of the spawning season. The presence of various groups of developing oocytes as occurs in *G. lineatus* and *S. politus* was termed asynchronism by Yamamoto and Yamazaki (1961) who found this condition common in fishes with long breeding seasons and multiple spawnings.

Another difference (Table 1) was the persistence of small quantities of Types 2 and 3 oocytes in *G. lineatus* after the conclusion of spawning in April which persist throughout summer. It is more typical for remaining vitellogenic oocytes to undergo atresia at the end of the spawning season as occurs in *S. politus* whose inactive ovaries contained only Type 1 oocytes (Table 2) from November to January. These low frequencies of mature summer *G. lineatus* oocytes may suggest spawning continued at a reduced frequency during this period. A more plausible explanation might be that these oocytes will ovulate early in the next spawning season. It thus appears that some early ovulating *G. lineatus* oocytes initiated yolk deposition late in the previous spawning season and remained over summer. It may be energetically advantageous for these yolk filled eggs to remain over summer as opposed to resorbing them.

As *G. lineatus* ranges from Baja California to British Columbia and *S. politus* from Baja California to Oregon (Miller and Lea 1972), my data may be useful for subsequent investigations to determine geographic variation in reproduction for these species.

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Literature Cited

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

SKOGSBERG, T.
1939. The fishes of the family Sciaenidae (croakers) of California. Calif. Dep. Fish Game, Fish Bull. 54, 62 p.

YAMAMOTO, K., AND F. YAMAZAKI.
1961. Rhythm of development in the oocyte of the goldfish, *Carassius auratus*. Bull. Fac. Fish., Hokkaido Univ. 12:93-110.

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FOOD OF FIVE SPECIES OF COOCCURRING FLATFISHES ON OREGON'S CONTINENTAL SHELF

The purpose of this paper is to describe and to compare the food of five flatfish species that actually cooccurred at one specific time and place on the central Oregon continental shelf: English sole, *Parophrys vetulus* Girard; rex sole, *Glyptocephalus zachirus* Lockington; rock sole, *Lepidopsetta bilineata* (Ayres); petrale sole, *Eopsetta jordani* (Lockington); and Pacific sanddab, *Citharichthys sordidus* (Girard). These demersal fishes are common along the west coast of North America, their ranges overlapping between southern California and the Gulf of Alaska (Hart 1973). *Parophrys vetulus*, *C. sordidus*, and *L. bilineata* occur mainly on the inner continental shelf. *Eopsetta jordani* is fished commercially on its feeding grounds (73-128 m), and in deep water (311-457 m) where spawning occurs (Forrester 1969). *Glyptocephalus zachirus* has a broad bathymetric range—it is common off Oregon and Washington from 90 to 550 m (Alverson et al. 1964). Off Oregon it was the second most numerous member of a species association ranging from 119 to 199 m, on an average sediment type of 69% sand, 19% silt, and 12% clay (Day and Pearcy 1968). In that same study, *C. sordidus* and *P. vetulus* composed 80.3% of a species association of fishes in shallower water (42-73 m) on a sandy bottom. According to Alverson (1960), *L. bilineata* is common on sandy or gravel bottom. The five flatfish species attain maximum sizes ranging from 410 mm for *C. sordidus* to 700 mm for *E. jordani* (Hart 1973).

Pearcy and Vanderploeg (1973) listed major food items—combined from several locations, seasons, and years—for most of the above species. That

study provided generalized information on food habits, but little insight into possible intra- or interspecific differences in diets resulting from actual interaction among cooccurring fishes. Our study is based on a single collection minimizing temporal and spatial variations associated with sampling. Food items were identified to species whenever possible. Thus, a detailed comparison of food taxa is arrived at with minimal geographic and no seasonal effects.

A trawl haul of 75 min total duration was made beginning at 1345 h Pacific daylight time, on 13 April 1975 with an Atlantic-Western trawl (24-m footrope) from the *Betty-A*, a commercial dragger, at approximately lat. 44°42'N, long. 124°24'W. Depth of water was 95-106 m. The sediment was sand (Byrne and Panshin 1968). Stomachs of fishes were removed and preserved in Formalin[1] at sea (Table 1). Food items were identified and enumerated in laboratories ashore.

TABLE 1.–Fishes captured in an Atlantic-Western trawl on 13 April 1975.

Species	No. caught	Total length range (mm)	No. examined	No. with stomach contents
Citharichthys sordidus	181	90- 377	62	26
Parophrys vetulus	50	230- 450	50	37
Glyptocephalus zachirus	24	240- 360	22	21
Eopsetta jordani	22	240- 510	12	7
Lepidopsetta bilineata	19	247- 474	19	15
Raja binoculata	9	940-1,460	8	6
Raja rhina	2	800- 890	2	1
Raja kincaidi	2	560- 570	2	0
Pleuronichthys verticalis	2	251- 254	2	1
Ophiodon elongatus	1	850	1	0
Squalus acanthias	1	1,000	0	—

Forage Organisms

All the food items identified from five species of flatfishes are listed in Table 2, and the major food taxa (taxa having a frequency of occurrence of 10% or more) are listed for individual fish of three species of flounders in Table 3.

Parophrys vetulus had a diverse diet, feeding primarily on polychaetes and amphipods. Mollusks, ophiuroids, and crustacea were also represented. The amphipod *Ampelisca macrocephala*, the most numerous single prey species, occurred in 60% of fish. The diversity of the diet of *P. vetulus* is due to the many different types of food consumed by individual fish (represented by the vertical columns in Table 3) rather than by different fish feeding on different prey. *Parophrys vetulus* appears to be an opportunistic feeder. Forrester (1969) reported polychaetes, clams, and ophiuroids as primary food organisms of *P. vetulus*, with incidental occurrences of sandlance, crab, amphipods, shrimp, squid, and small fish. Pearcy and Vanderploeg (1973) found polychaetes, amphipods, and pelecypods were important prey of *P. vetulus* off Oregon.

Glyptocephalus zachirus fed primarily on four species of amphipods and secondarily on polychaetes. Amphipods occurred in all but one stomach, polychaetes in 71% of the stomachs with food. Nematodes were encountered in 38% of the stomachs but were probably parasitic (Robert Olson, pers. commun.). Pearcy and Vanderploeg (1973) also found polychaetes and amphipods to be the major food of *G. zachirus* off Oregon.

The principal food of *Lepidopsetta bilineata* was ophiuroids. All but one individual had been feeding on *Ophiura*, which constituted the bulk of the stomach contents. A few polychaetes and mollusks were also present. According to Shubnikov and Lisovenko (1964), the basic items of its diet are polychaetes, mollusks, shrimps, and other crustaceans. Fishes (sandlance) and echinoderms were occasionally found in stomachs. Food items reported for *L. bilineata* in Hecate Strait, British Columbia, by Forrester and Thomson (1969) were clams, polychaetes, crabs, shrimps, sandlance, herring, echinoderms, and amphipods.

Eopsetta jordani preyed on fishes and decapod crustaceans. Polychaetes and amphipods were not present in its diet. Ketchen and Forrester (1966) found euphausiids, herring, sandlance, and shrimp as major food items in stomachs of *E. jordani*. Pearcy and Vanderploeg (1973) reported shrimps, pelagic fishes, and euphausiids as major food items, indicating that this species feeds largely on pelagic prey.

Citharichthys sordidus had been feeding intensively on the northern anchovy, *Engraulis mordax*. Anchovy were noted in nearly all the sanddab when stomachs were removed, and all intact preserved stomachs contained them. Since anchovy were not caught in the otter trawl, feeding in the net is thought to be unlikely. According to Pearcy and Vanderploeg (1973), euphausiids, shrimps, amphipods, and crab larvae were common in *C. sordidus* stomachs.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.–Taxa identified from stomach contents of five species of Pacific Northwest flatfishes.[1]

Taxa	*Parophrys vetulus*	*Glyptocephalus zachirus*	*Lepidopsetta bilineata*	*Eopsetta jordani*	*Citharichthys sordidus*
POLYCHAETA	94.6	71.4	40.0		
Aphroditidae					
Aphrodita negligens			x		
Capitellidae					
[2] Capitellidae spp.	10.8				
[2] *Notomastus* spp.	x				
Chaetopteridae spp.	x				
Cirratulidae					
Cirratulidae spp.	40.5				
Chaetozone setosa	x				
Chaetozone spp.	x				
Tharyx spp.	x				
Goniadidae					
Goniadidae spp.	x	x			
Glycinde picta (?)	13.5				
Lumbrineriidae					
Lumbrineris spp.	18.9				
Magelonidae					
Magelona spp.	x				
Maldanidae spp.	x				
Nephtyidae					
Nephtys caecoides	x				
Nephtys spp.	43.2				
Onuphidae					
Nothria geophiliformis (?)	x				
Nothria iridescens (?)	10.8	14.3	13.3		
Nothria spp.		19.0			
Opheliidae					
Opheliidae spp.		9.5			
Ammotrypane aulogaster	8.1				
Orbiniidae					
Haploscoloplos spp.	x				
Oweniidae					
Myriochele oculata	16.2				
Myriochele spp.	10.8				
Owenia spp.	16.2				
Paraonidae spp.	21.6				
Pectinariidae					
Pectinaria spp.	x	x	x		
Phyllodocidae					
Eteone longa	x				
Polynoidae spp.			13.3		
Sigalionidae					
Sigalionidae spp.	18.9				
Thalenessa spinosa	x				
Spionidae spp.	18.9				
Terebellidae					
Terebellidae spp.	35.1				
Polycirrus spp.	x				
Unidentified	x	x			
GASTROPODA	13.5				11.1
Cylichna attonsa	10.8				
Mitrella gouldii	x				
Mitrella spp. (?)					11.1
PELECYPODA	27.0	9.5	13.3		
Acila castrensis		x			
Axinopsida serricata	x				
Cardiomya oldroydi	x				
Nucula tenuis	16.2				
Macoma spp.	x				
Tellina carpenteri (?)	8.1		13.3		
Unidentified	x				
SCAPHOPODA	16.2	4.8			
Dentalium sp.	13.5				
Unidentified fragment	x				
Scaphopoda(?)		x			
CEPHALOPODA					11.1
Octopoda					11.1
Beak of *Loligo* spp. (?)					11.1
CRUSTACEA	91.9	100.0	6.7	28.6	33.3
Cypris larvae (?)	x				
Copepoda (calanoid)	10.8				
Mysidacea					
Neomysis spp.					11.1
Unidentified				14.3	
Ostracoda (?)	x				
Cumacea	10.8				
Tanaidacea	x				

TABLE 2.–Continued.

Taxa	*Parophrys vetulus*	*Glyptocephalus zachirus*	*Lepidopsetta bilineata*	*Eopsetta jordani*	*Citharichthys sordidus*
Euphausiacea					
Euphausia pacifica					22.2
Decapoda					
Natantia					
Crangon spp.					11.1
Nectocrangon spp.				14.3	
Unidentified shrimp					x
Reptantia					
Pagurus samuelis			x		
Mursia spp.				14.3	
Crab leg		x			
Amphipoda	83.8	95.2			
Ampeliscidae					
Ampelisca cristata		x			
Ampelisca macrocephala	59.5	33.3			
Ampelisca spp.	x				
Amphilochidae spp. (?)	x				
Aoridae					
Lembos spp.	x				
Argissidae					
Argissa hamatipes	x				
Isaeidae					
Photis brevipes	x	x			
Protomedeia spp.	x				
Lysianassidae					
Lysianassidae spp.	x				
Acidostoma spp.		x			
Anonyx anivae	x				
Hipomedon wecomus	18.9	28.6			
Oedicerotidae					
Monoculodes emarginatus	x				
Monoculodes sp. #1	x	x			
Synchelidium shoemakeri	x	x			
Westwoodilla caecula	x				
Phoxocephalidae					
Paraphoxus abronius	x				
Paraphoxus daboius (?)	x				
Paraphoxus epistomus (?)	21.6	33.3			
Paraphoxus fatigans	10.8	4.8			
Paraphoxus lucubrans	x				
Paraphoxus milleri		x			
Paraphoxus obtusidens	16.2	33.3			
Paraphoxus variatus	x				
Paraphoxus spp.	10.8				
Pleustidae					
Pleustidae spp.		x			
Pleusymtes coquilla		x			
OPHIUROIDEA	83.8		93.3		
Amphiodia periercta	10.8				
Amphiodia urtica	10.8				
Amphiuridae spp.	10.8				
Ophiura lutkeni	35.1		73.3		
Ophiura sarsii	x				
Ophiura spp.	8.1		20.0		
PISCES		9.5		100.0	100.0
Agonidae				14.3	
Engraulis mordax				14.3	100.0
Glyptocephalus zachirus				14.3	
Radulinus spp.				14.3	
Unidentified		x		x	
Fish scale	x	x			
NEMERTINEA	13.5				
NEMATODA	x	x			
SIPUNCULIDA	2.7		13.3		
ECHIURIDA		x			
ACANTHOCEPHALA		x			
Miscellaneous					
Gastropod egg case	x				
Egg mass	x				
Lenses					x
Unidentified remains	x	x			

[1]Frequency of occurrence is given as a percentage for food taxa whenever these taxa occur in 10% or greater of any of the five species of fishes. Ophelidae were significant on a weight basis in *G. zachirus*, and were combined with *Ammotrypane aulogaster* for calculation of similarity. An "x" denotes any other occurrence.

[2]Taxa enclosed within brackets were treated as a single group in Table 3.

TABLE 3.—Numbers of food items of major[1] taxa in contents of individual fish stomachs. Each vertical column represents one stomach.

| Fish species and taxa | Number of food items | | |

similarity among the food habits of the three fishes that preyed on benthic invertebrates was calculated using commonly occurring prey (Table 3) and Horn's (1966) measure of niche overlap. The overlap was largest between *P. vetulus* and *G. zachirus* (C_λ = 0.40). This is because both fishes fed on the same species of amphipods and the polychaete *Nothria iridescens*. *Parophrys vetulus* preyed on a very diverse array of invertebrate taxa, while *G. zachirus* appeared to be more selective in its feeding.

The amount of food overlap among the other species pairs was low (0.19 between *P. vetulus* and *L. bilineata* and only 0.03 between *G. zachirus* and *L. bilineata*). These low values are explained by the high occurrence of *Ophiura lutkeni* only in *L. bilineata*. Also, *L. bilineata* fed on members of two scaleworm families, Aphroditidae and Polynoidae, neither of which is represented in the other flatfishes.

The food habits of the flatfishes that we found to be mainly piscivorous were also different. *Eopsetta jordani* preyed on various fishes, including benthic agonids, pleuronectids, and cottids, as well as a benthic shrimp and crab, whereas *C. sordidus* fed almost exclusively on the pelagic *Engraulis mordax*.

Partitioning of the food resources among the five flatfish species is obvious from our data—the different, syntopic species fed upon different organisms. According to MacArthur and Pianka (1966), a more productive environment should lead to a more restricted diet in terms of different species eaten, but in a patchy environment this does not apply to predators that spend most of their time searching. If the bottom occupied by *P. vetulus* is inhabited by patches of invertebrates, then this species might be such a scavenging "generalist" predator. Rae (1969) documented a food interaction similar to the one in this study between the lemon sole, *Microstomus kitt*, and witch, *Glyptocephalus cynoglossus*, off Scotland. The witch, restricted to muddy bottoms, fed on a more restricted fauna than the lemon sole, whose diet included the hard-bottom species typical of its habitat in addition to species from muddy-bottom types.

Differences in time of feeding could also account for differences in the species composition of prey. Diel changes in the habits of prey can serve to increase or decrease their exposure to predators, and hence their availability as food (Hobson 1965; Jones et al. 1973). More so than the other species, the stomach contents of *G. zachirus* were in a late stage of digestion, suggesting that they had fed a longer time before capture than other species.

The diet of fishes is related not only to their feeding behavior but also to their digestive morphology and mouth structure. The size of the mouth relative to body length correlated with the size of food organisms for bothid flounders in Georgia coastal waters (Stickney et al. 1974). Symmetry of the jaws plays an important role in the mode of feeding, as species with symmetrical jaws generally take free-swimming food, while those with asymmetrical jaws are mainly bottom feeders (Yazdani 1969). Flatfishes that feed on polychaetes and mollusks typically have smaller stomachs, larger intestines, and smaller gill rakers with fewer teeth than flatfishes that feed on other fishes (DeGroot 1971; Tyler 1973). The mouths of *P. vetulus*, *G. zachirus*, and *L. bilineata* are small,[2] the jaws and dentition are better developed on the blind side (i.e., asymmetrical), the teeth are incisorlike (bluntly conical in *L. bilineata*), and the gill rakers are without teeth. These morphological adaptations correlate with the preponderance of benthic invertebrates in their diets. The piscivores, *E. jordani* and *C. sordidus*, on the other hand, have larger mouths,[3] nearly symmetrical jaws with sharp teeth, and long gill rakers with teeth.

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Literature Cited

ALVERSON, D. L.
1960. A study of annual and seasonal bathymetric catch

[2]Length of maxillary into head on ocular side is 4¼-4⅓, 4½-5¼, and 3½-4⅓, respectively (Norman 1934); also see Norman for line drawings depicting the relative mouth size of flatfishes discussed in this paper.

[3]Length of maxillary into head is about 2⅓ and 2¾ (nearly 3), respectively (Norman 1934).

patterns for commercially important groundfishes of the Pacific Northwest coast of North America. Pac. Mar. Fish. Comm. Bull. 4:1-66.

ALVERSON, D. L., A. T. PRUTER, AND L. L. RONHOLT.
1964. A study of demersal fishes and fisheries of the northeastern Pacific Ocean. H. R. MacMillan Lectures in Fisheries, Inst. Fish., Univ. B.C., 190 p.

BYRNE, J. V., AND D. A. PANSHIN.
1968. Continental shelf sediments off Oregon. Oreg. State Univ. Sea Grant Ext. Mar. Advis. Program 8, 4 p.

DAY, D. S., AND W. G. PEARCY.
1968. Species associations of benthic fishes on the continental shelf and slope off Oregon. J. Fish. Res. Board Can. 25:2665-2675.

DEGROOT, S. J.
1971. On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces: Pleuronectiformes). Neth. J. Sea Res. 5:121-196.

FORRESTER, C. R.
1969. Life history information on some groundfish species. Fish. Res. Board Can., Tech. Rep. 105, [17 p.]

FORRESTER, C. R., AND J. A. THOMSON.
1969. Population studies on the rock sole (*Lepidopsetta bilineata*) of northern Hecate Strait, British Columbia. Fish. Res. Board Can., Tech. Rep. 108, 104 p.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.

HOBSON, E. S.
1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965:291-302.

HORN, H. S.
1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100:419-424.

JONES, D. A., N. PEACOCK, AND O. F. M. PHILLIPS.
1973. Studies on the migration of *Tritaeta gibbosa*, a subtidal benthic amphipod. Neth. J. Sea Res. 7:135-149.

KETCHEN, K. S., AND C. R. FORRESTER.
1966. Population dynamics of the petrale sole, *Eopsetta jordani*, in the waters of western Canada. Fish. Res. Board Can., Bull. 153, 195 p.

MACARTHUR, R. H., AND E. R. PIANKA.
1966. On optimal use of a patchy environment. Am. Nat. 100:603-609.

NORMAN, J. R.
1934. A systematic monograph of the flatfishes (Heterosomata). Vol. I. Psettodidae, Bothidae, Pleuronectidae. Br. Mus. (Nat. Hist.), Lond., 459 p.

PEARCY, W. G., AND H. A. VANDERPLOEG.
1973. Radioecology of benthic fishes off Oregon. *In* Radioactive contamination of the marine environment, p. 245-261. Int. At. Energy Agency, Vienna.

RAE, B. B.
1969. The food of the witch. Mar. Res. Dep. Agric. Fish. Scotl. 2, 23 p.

SHUBNIKOV, D. A., AND L. A. LISOVENKO.
1964. Data on the biology of rock sole of the southeastern Bering Sea. Tr. Vses. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 49 (Izv. Tikhookean. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 51): 209-214. (Transl. in Soviet Fisheries Investigations in the Northeast Pacific, Part II, p. 220-226, by Israel Program Sci. Transl., 1968, available Natl. Tech. Inf. Serv., Springfield, VA, as TT 67-51204.)

STICKNEY, R. R., G. L. TAYLOR, AND R. W. HEARD III.
1974. Food habits of Georgia estuarine fishes. I. Four species of flounders (Pleuronectiformes: Bothidae). Fish. Bull., U.S. 72:515-525.

TYLER, A. V.
1973. Alimentary tract morphology of selected North Atlantic fishes in relation to food habits. Fish. Res. Board Can., Tech. Rep. 361, 23 p.

YAZDANI, G. M.
1969. Adaptations in the jaws of flatfish (Pleuronectiformes). J. Zool. (Lond.) 159:181-222.

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AGE DETERMINATION OF A TROPICAL REEF BUTTERFLYFISH UTILIZING DAILY GROWTH RINGS OF OTOLITHS

The recent economic expansion of the aquarium fish industry in Hawaii has raised questions concerning the judicious exploitation of reef resources (Pellegrin 1973; Randall 1973; Reese 1973). However, appropriate management strategies cannot be implemented until sufficient biological data have been gathered, allowing a characterization of exploited populations of fishes. The relative paucity of such information concerning the vast majority of reef species underscores the need for future research.

Studies pertaining to the age and growth of fishes are especially useful in the analysis of exploited stocks. Unfortunately, efforts to age tropical fishes in the past have proved to be largely unsuccessful and/or involve considerable expenditures in time and effort (Pannella 1974). However, the recent studies of Pannella (1971, 1974) have initiated the development of a technique for determining the age of tropical fishes without having to resort to more elaborate approaches such as the Peterson method of ageing. Panella has provided evidence that many species of both temperate and tropical fishes deposit lamellae on their otoliths with a diel periodicity. These lamellae are visible as rings or circuli after the otolith has been properly prepared. In the absence of annuli, these rings may be used to age fish. A recent investigation by Struhsaker and Uchiyama (1976) using this technique was successful in ageing the Hawaiian

anchovy (*Stolephorus purpureus*) and in showing the daily nature of these lamellae.

This paper reports on studies of the age and growth of the Hawaiian endemic millet-seed butterflyfish, *Chaetodon miliaris* Quoy and Gaimard (Perciforms: Chaetodontidae), using this approach. Butterflyfishes are exceptionally attractive and are heavily exploited by the aquarium industry in Hawaii. This study was initiated in order to obtain information useful to state regulatory agencies in the management of reef fish stocks.

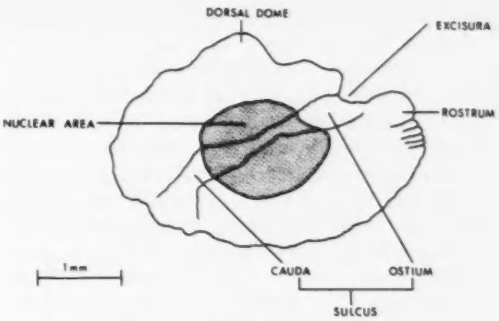

FIGURE 1.–Schematic representation of the left sagitta of a 94-mm *Chaetodon miliaris* viewed medially.

Methods

All fish were collected by spearing around the island of Oahu, Hawaii, during 1974 and were measured to the nearest millimeter standard length (SL) while still fresh. Next, the otoliths were extracted by means of a horizontal section through the cranium above the eyes. Of the three otoliths on each side, only the largest, the sagitta, was studied. Figure 1 depicts a left sagitta of a 94-mm *C. miliaris* viewed medially. After both sagittae were removed, all membranes and endolymph were carefully teased way under a dissecting microscope. The otoliths were then rinsed in water and placed in a 2% aqueous solution of HCl for several minutes of etching. They were then rinsed again, thoroughly dried, and finally mounted in depressions of glass slides where they were immersed in euparal (an aromatic oil which acts as a clearing agent) and covered with glass cover slips. After clearing for 2 wk, the otoliths were ready for reading. Otoliths were read from the nucleus outward along their long axis with a compound binocular microscope utilizing transmitted light at a magnification of 400× (Figure 2). The rings in each sagitta were counted twice, using a hand counter, and the average of the four readings obtained from each specimen was used to estimate the age of the fish in days.

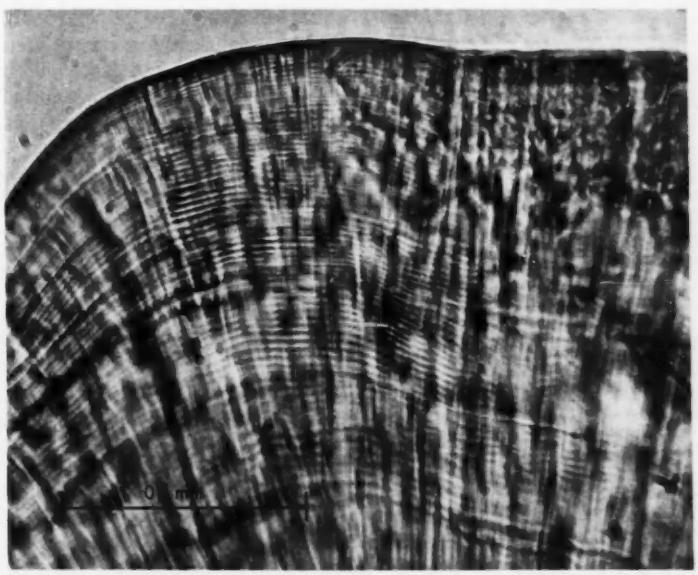

FIGURE 2.–Internal ring structure of the otolith of *Chaetodon miliaris* specimen number 11. Not all the rings are visible in this photograph.

Results

The counts of rings within otoliths are summarized in Table 1. The average number of rings for each fish has been rounded to the nearest integer.

On the assumption that one ring is equal to one day's growth (Pannella 1971, 1974; Struhsaker and Uchiyama 1976), the data were fitted to the von Bertalanffy growth equation employing the techniques of Allen (1966). This model states:

$$l_t = L_\infty (1 - e^{-K(t - t_0)}) \quad (1)$$

where l_t = length at time t
L_∞ = the average length of a group of fish grown for an infinite period of time
K = a growth parameter which describes the rate at which l_t is approaching L_∞
t_0 = the back calculated X intercept or the time at which size was zero.

The data are plotted along the calculated von Bertalanffy growth curve in Figure 3. The calculated growth equation for the data in this report is:

$$l_t = 127(1 - e^{-0.0031(t+30)}) \quad (2)$$

when size is expressed as SL in millimeters and time is expressed in days. Alternatively, when time is expressed in years, the equation becomes:

$$l_t = 127(1 - e^{-1.13(t+0.082)}). \quad (3)$$

The estimated asymptotic size of 127 mm SL is a reasonable figure. Of 345 *C. miliaris* examined in another study (Ralston 1975), 4 were larger than this size. Of those, three were 131 mm SL or less,

TABLE 1.–The number of rings counted in the otoliths of *Chaetodon miliaris* collected around Oahu, Hawaii, 1974.

Specimen	Date of capture	Standard length (mm)	Mean number of rings	Range of counts
1	7 June	27	35	32-38
2	18 June	29	71	65-74
3	7 June	32	51	48-52
4	11 July	35	108	99-115
5	11 July	42	133	124-138
6	1 Oct.	44	118	110-122
7	5 Oct.	50	115	107-121
8	1 Oct.	52	138	134-141
9	5 Oct.	56	147	141-153
10	5 Oct.	66	169	162-178
11	5 Oct.	70	227	215-238
12	5 Oct.	71	228	219-235
13	5 Oct.	71	221	216-227
14	1 Dec.	86	322	307-333
15	1 Dec.	87	375	362-391

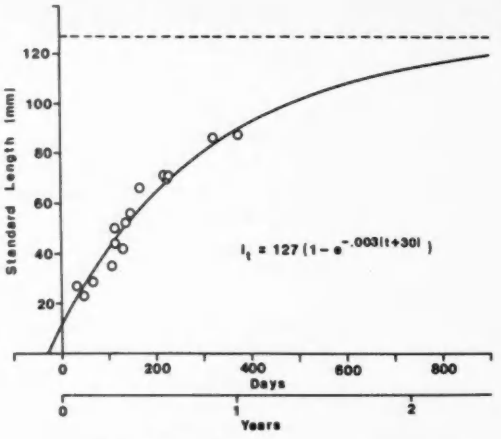

FIGURE 3.–The von Bertalanffy growth curve in length fitted to 15 individuals of *Chaetodon miliaris* aged by means of otoliths.

while the fourth was 137 mm SL. Because L_∞ can be thought of as an average, if sampling is intensive enough, one would expect to find individuals of a larger size. Of all the fish sampled in this earlier study, only 1.2% were larger than the estimated growth ceiling of the von Bertalanffy model as determined from the otoliths of the 15 individuals reported on here.

The growth of *C. miliaris* is very fast. The estimated growth parameter, K, of the von Bertalanffy equation describes how quickly growth proceeds. Large values of K are associated with rapid growth. Beverton and Holt (1959) presented values of K for 57 species of fishes and of those, only 6 species have K values exceeding that of *C. miliaris*.

It should also be noted that only fish which were less than 90 mm SL are reported on here. It was found that the otoliths of larger fish became increasingly difficult to read. Not only do the otoliths become thicker, but the peripheral ring increments become smaller with growth. For these reasons, larger fish could not be reliably aged in this study.

Discussion

On 2 August 1966, Wass (1967) defaunated a small patch reef in Kaneohe Bay, Hawaii, while studying the repopulation rates of various species of fishes. In so doing, he sampled 476 *C. miliaris* in 1 day. He gave a size-frequency distribution,

suitable for the Peterson method of ageing, which is reproduced in Figure 4.

The first mode centered on 7 cm total length (TL) could well represent a recently recruited cohort. A size of 70 mm TL corresponds to a length of 58 mm SL for *C. miliaris* (Ralston 1975). Spawning in this species is known to occur between December and April but peaks around the end of February or the beginning of March (Ralston 1975). Consequently, about 155 days elapsed between the time of peak spawning for this species and the date of capture of these 476 specimens. Assuming growth according to Figure 3, after 155 days of growth, juvenile *C. miliaris* are estimated to be 55 mm SL. This size corresponds closely with the first mode of Wass' size-frequency distribution (58 mm SL or 70 mm TL), thus corroborating Figure 3.

Further evidence in support of the von Bertalanffy growth curve and therefore, the interpretation of otolith ring patterns, comes from examining the size at which *C. miliaris* first reproduce. Ralston (in press) reported that both male and female *C. miliaris* reached reproductive maturity at a size of about 90 mm SL. Referring to Figure 3, fish of this size are about 1 yr old. If spawning is periodic, as it is in *C. miliaris* (Ralston 1975), one expects the onset of reproductive maturity to occur after some multiple of the interval between spawning periods has elapsed. One year is one such interval and *C. miliaris* becomes reproductive during the first spawning season after birth.

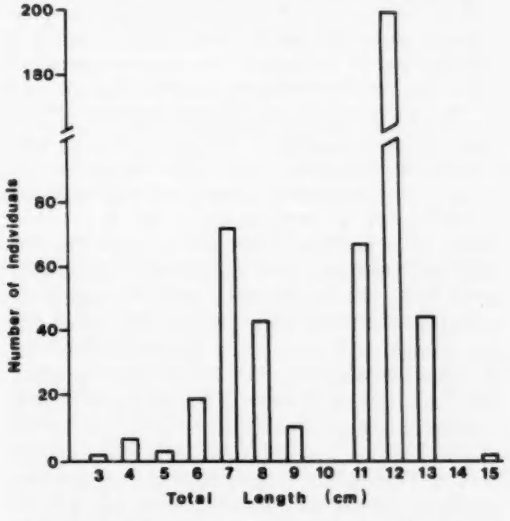

FIGURE 4.—Size-frequency distribution of *Chaetodon miliaris* collected by Wass (1967) in Kaneohe Bay. (Redrawn from his figure 7.)

Evidence presented here in the form of interpretation of the data of Wass (1967) and examination of age at maturity substantiate the growth of *C. miliaris* as described by the von Bertalanffy curve of Figure 3. These in turn confirm the accuracy and utility of employing the diel lamellae in the otoliths of fishes as growth chronometers. Although a new and as yet somewhat untried technique, Pannella's method of age determination offers the potential to age fishes in situations where this was not feasible in the past.

Acknowledgments

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Literature Cited

ALLEN, K. R.
1966. A method of fitting growth curves of the von Bertalanffy type to observed data. J. Fish. Res. Board Can. 23:163-179.

BEVERTON, R. J. H., AND S. J. HOLT.
1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. *In* G. E. W. Wolstenholme and M. O'Connor (editors), Ciba Foundation Colloquia on Ageing 5:142-177. J. & A. Churchill Ltd., Lond.

PANNELLA, G.
1971. Fish otoliths: daily growth layers and periodical patterns. Science (Wash., D.C.) 173:1124-1127.
1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes. *In* T. B. Bagenal (editor), Proceedings of an International Symposium on the Ageing of Fish, p. 28-39. Unwin Brothers Ltd., Surrey, Engl.

PELLEGRIN, D.
1973. Curbs urged in collecting tank fish. Honolulu Advertiser, Sept. 6.

RALSTON, S.
1975. Aspects of the age and growth, reproduction, and diet

of the millet-seed butterflyfish, *Chaetodon miliaris* (Pisces: Chaetodontidae), a Hawaiian endemic. M.S. Thesis, Univ. Hawaii, Honolulu.

In press. Anomalous growth and reproductive patterns in populations of *Chaetodon miliaris* (Pisces: Chaetodontidae) from Kaneohe Bay, Oahu. Pac. Sci.

RANDALL, J. E.

1973. Marine parks seen as key to reef beauty. Honolulu Advertiser, Sept. 5.

REESE, E.

1973. Collectors as a threat to reef fishes. Honolulu Star-Bulletin, May 15.

STRUHSAKER, P., AND J. H. UCHIYAMA.

1976. Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae) from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 74:9-17.

WASS, R.

1967. Removal and repopulation of the fishes on an isolated patch coral reef in Kaneohe Bay, Hawaii. M. S. Thesis, Univ. Hawaii, Honolulu.

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AN EPIBENTHIC SAMPLER USED TO STUDY THE ONTOGENY OF VERTICAL MIGRATION OF *PANDALUS JORDANI* (DECAPODA, CARIDEA)[1]

Pandalus jordani Rathbun, like many other species of pandalid shrimps, undergo regular diel changes in their vertical distribution (Tegelberg and Smith 1957; Alverson et al. 1960; Pearcy 1970, 1972; Robinson in press). Little is known, however, about the vertical distribution and diel migrations of larval and juvenile shrimp, or at what stage of the life history vertical migration and benthic existence are initiated.

Berkeley (1930) found that size or age of larval *P. danae* increased with increasing depth in a semienclosed embayment in British Columbia. Pearcy (1972) published the only information on day/night differences in benthic occurrence of juvenile *P. jordani*. Using a plankton net mounted on a beam trawl, he collected more juveniles (<7.0 mm in carapace length) near the bottom during day than night.

In order to sample the water column completely, it was necessary to supplement plankton tows with a discrete, quantitative sample on or just off the bottom. Various methods have been used for this purpose but we thought that all of them were inadequate for the present study. Many epibenthic samplers do not have an opening/closing device and therefore are subject to contamination from the water column above (Russell 1928; Frolander and Pratt 1962; Pearcy 1972; Beardsley 1973). Others are only capable of collecting small samples, in relatively shallow water (Clutter 1965; Macer 1967). In others the opening/closing device seems inefficient or overly complex (Bossanyi 1951; Wickstead 1953; Macer 1967; Hesthagen 1970). Design criteria for the sampler used in this study were: a simple, substrate activated, opening/closing device capable of quantitatively sampling in depths greater than 150 m and sampling at least 500 m^3 of water with no loss of filtration efficiency.

Epibenthic Sampler Design

The epibenthic sampler consists of a sled and a box, to which are attached a plankton net and a substrate-actuated opening/closing device (Figure 1). The frame of the sled was welded from flat steel strap (5.1 × 0.6 cm). The runners (23 × 0.6 cm mild steel plate) are joined across the front by a piece of the same steel bent to conform to the front of the sled. This serves to carry the sled over small obstructions on the seabed and further protect the door of the box when it is in the open position. A bumper bar (5.1 × 0.6 cm) was also fitted across the front of the sled to prevent large obstacles from entering the mouth of the sampler. Two brackets on either side of the sled serve as attachment points for the box. The six different positions allow the box to be positioned from 2.5 to 22.9 cm off the bottom. Two pieces of strap (5.1 × 0.6 cm) were welded along the top of the frame with nine holes to provide various attachment points for the towing bridle. In addition, four pairs of towing points were placed around the front of the frame.

The box (106.7 × 45.7 × 53.3 cm), made of 3.2-mm mild steel plate, is reinforced in front by steel strap (2.5 × 0.32 cm), forming a lip around the mouth of the box (Figure 1B). The box is further reinforced by L stock (2.5 × 0.32 cm) placed around the box 10 cm from the rear edge. Attach-

[1]This research was supported in part by Grant No. 04-5-158-2, Office of Sea Grant, National Oceanic and Atmospheric Administration, U.S. Department of Commerce.

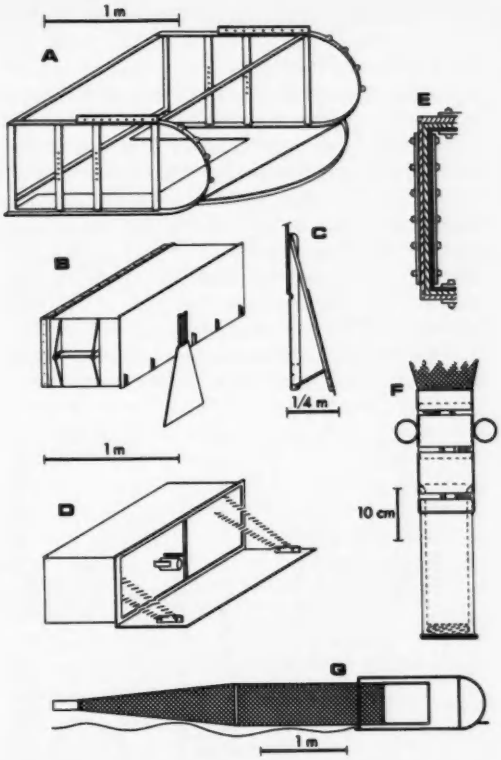

FIGURE 1.–Opening/closing epibenthic sampler: A) sled frame; B) box with door closed; C) detail, side view of shoe, hinge, and shoe adjustment device; D) box with door open showing flowmeter and springs for closing door; E) schematic net attachment, solid line is box wall, two cross hatched lines are collars of coarse mesh liner (inner) and plankton net (outer), open bars are stainless steel straps with bolts; F) safety collar insert with rings for cable attachment protruding through collar and PVC cod end with threaded teflon plug; G) schematic lateral view showing sled, box, net, and canvas chafing gear.

ment points for affixing the box to the sled were made from 3.8-cm round stock, tapped to 9.5 mm and reinforced with 5.1 × 0.48 cm flat stock. The box is fastened to the sled by four stainless steel bolts (0.95 × 3.8 cm).

The door of the box was made from mild steel plate (109.2 × 48.3 × 0.48 cm) and is hinged with a 6.4-mm stainless steel rod at five points along the bottom. The shoe which opens the door upon contact with the sea floor is triangular shaped (33.0 × 50.8 × 0.48 cm) and is hinged to allow adjustment, depending on the distance the box is set off the bottom (Figure 1C). Four large springs (5.1 × 22.9 cm), attached internally, pull the door shut when the sled leaves the sea floor (Figure 1D). The door-to-shoe surface area ratio is about 5:1, so that water pressure effectively holds the door shut on descent and ascent (Figure 1B). A TSK flowmeter[2] is mounted in the middle of the mouth by a brace (1.9 × 0.48 cm). The nets are attached to the rear of the box by sandwiching them between stainless steel straps (5.1 × 0.48 cm) bolted together at 7.6-cm intervals (Figure 1E). The inner strap has 6.4-mm stainless steel bolts welded to it, while the outer strap has holes drilled to correspond to the bolts in the inner strap, as well as the holes in the box and net collars. The entire sled, except for the springs and stainless steel fittings, was hot dipped galvanized.

The plankton net was made of 571-μm mesh nylon monofilament. The filtering area to mouth area ratio is 9:1. The "cylinder"/"cone" net had a total mesh area of 7.7 m^2, with 2.6 m^2 in the cone and 5.1 m^2 in the cylinder. The collars were made of plastic coated nylon webbing. The cod end is a 30.5-cm piece of 10.2 cm outside diameter schedule 80 polyvinyl chloride (PVC) pipe, with a threaded teflon plug for removing the sample. There is also a stainless steel insert above the cod end fitted with two rings protruding through slits in the collar, for attachment of safety wires from the sled frame to the cod end, in the event a large amount of sediment was retained (Figure 1F). Overall length of the net including collars and cod end is 5.1 m (Figure 1G). A small coarse mesh net 1 m deep (2.5-cm stretched mesh) was mounted inside the plankton net (see Figure 1E) to catch any large animals or objects and prevent them from damaging the plankton net or the sample in the cod end. A piece of heavy canvas (1.2 × 3.7 m, no. 4 duck) was attached to the rear of the sled by shackles, to protect the plankton net from chafing on the sea floor (Figure 1G).

Epibenthic Sampler Operation

Because of its size and weight (ca. 150 kg in air) the epibenthic sampler can only be used from a vessel with a suitable trawl winch; in the present study the 24.4-m RV *Cayuse* with a 9.5-mm diameter trawl wire was used. The sled was fastened to the trawl wire with a ball bearing swivel and a 3-m bridle of 9.5-mm wire attached to the

[2]Tsurumi-Seiki Kosakusho. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

second set of attachment points from the front of the sled. From these towing points the sled proved to be stable, never landing on the bottom upside down. It could be launched and recovered by two people in moderate-to-rough seas. The sled was launched while underway at 2 knots. A 20-min tow (bottom time) at 2 knots was calculated to be sufficient to filter 500 m^3 of water. Presence on the bottom was detected by the winch potentiometer.

Filtering efficiency of the sampler, based on the degree of clogging, was never markedly reduced over this time interval. However on soft muddy-sand bottoms, characteristic of *P. jordani* grounds, bottom times were reduced to 10 min because of the amount of fine sediment and meiofauna stirred up and retained in the cod end. Large organisms, including adult *P. jordani*, as well as the fragile urchin, *Allocentrotus fragilis*, and slender sole, *Lyopsetta exilis*, were effectively retained in the coarse mesh liner and prevented from reaching the sample in the cod end. Flowmeter readings indicated that at no time did the number of animals retained in the liner seriously occlude the mouth of the plankton net and affect its efficiency. On coarse sand bottoms, the samples were very clean, with little sediment and meiofauna retained, even when the net was only 5-8 cm off the bottom.

Though the sled was never observed firsthand while on the bottom, evidence from skid marks on the runners and shoe, behavior of the potentiometer while the sled was on the bottom, and the relationship between flowmeter readings and bottom time indicated that the epibenthic sampler was stable and not prone to dig in or bounce off the bottom while being towed.

Vertical Distribution of Larval *Pandalus jordani*

On 30 and 31 May 1972 the epibenthic sampler was used to sample near-bottom fauna and open bongo nets were used to obtain a series of quasi-vertically stratified plankton samples 10 nautical miles off Cascade Head, on the central Oregon coast (lat. 45°04.0'N, long. 124°15.1'W). The 0.7-m diameter bongo frames had paired cylidner/cone 571-μm Nitex nets, 5.1 m in length with an effective filtering area to mouth area ratio of 8:1. A scope to depth ratio of 2:1 was maintained by using a 40-kg multiplane kite otter as a wire depressor (Colton 1959). All nets contained TSK flowmeters. A time-depth recorder was fixed to the wire just above the bongo nets. Tows were made at four strata (0-10, 11-50, 51-100, 101-150 m) with the open bongo nets, and a bottom sample was taken with the epibenthic sampler at 160 m. Replicate tows were taken at each depth interval, both day (1200-1930 h) and night (2105-0400 h). Contamination in the open bongo net was minimized by lowering to the depth interval as fast as possible, doing a stepped oblique tow through the horizon, and then raising the net as quickly as possible. Towing time at depth was long enough to keep the period of contamination below 20% of the total sampling time for the deepest tows.

The vertical distribution of *P. jordani* larvae and juveniles is summarized in Figure 2. During

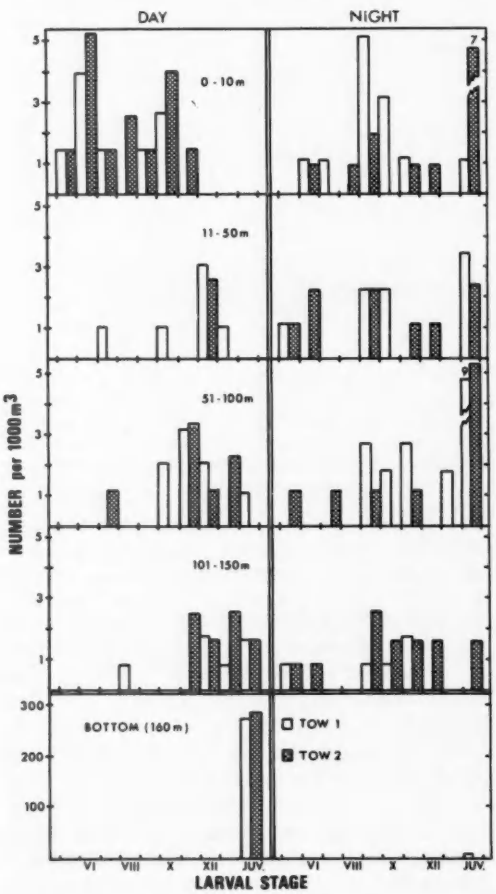

FIGURE 2.–Vertical distribution of larvae and early juvenile *Pandalus jordani*, during one day and one night period. All tows were replicated.

the day, larvae were distributed throughout the water column and were most abundant in the 0- to 10-m depth interval. A trend of increasing age with depth was evident. Early juveniles were present in low numbers in the 51- to 100-m and 101- to 150-m intervals. The sled tows revealed a very high concentration of early juveniles (284 and 290/1,000 m^3) on the bottom during midday.

At night larval shrimp were still distributed throughout the entire water column. The younger stages (V and VI), found in some abundance in the 0- to 10-m interval during the day, were not collected at night. Furthermore, an age gradient with depth was no longer present. This was due, in part, to the presence of late larvae at all depths in the water column. The most dramatic feature of the night distribution was the vertical migration of the early juveniles as indicated by their virtual absence on the bottom (0 and 4/1,000 m^3) in the sled samples. Juveniles were again present in the lower portion of the water column (101-150 m) and had migrated into the upper 100 m, including the top 10 m. There was no evidence that larvae younger than Stage XIII migrated to any extent. Vertical migratory behavior starts late in the larval phase, before the molt to juvenile and recruitment to the bottom.

Acknowledgments

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Literature Cited

ALVERSON, D. L., R. L. MCNEELY, AND H. C. JOHNSON.
1960. Results of exploratory shrimp fishing off Washington and Oregon (1958). Commer. Fish. Rev. 22(1):1-11.

BEARDSLEY, A. J.
1973. Design and evaluation of a sampler for measuring the near-bottom vertical distribution of pink shrimp, *Pandalus jordani*. Fish. Bull., U.S. 71:243-253.

BERKELEY, A. A.
1930. The post-embryonic development of the common pandalids of British Columbia. Contrib. Can. Biol. 6:79-163.

BOSSANYI, J.
1951. An apparatus for the collection of plankton in the immediate vicinity of the sea-bottom. J. Mar. Biol. Assoc. U.K. 30:265-270.

CLUTTER, R. I.
1965. Self-closing device for sampling plankton near the sea bottom. Limnol. Oceanogr. 10:293-296.

COLTON, J. B., JR.
1959. The multiplane kite-otter as a depressor for high-speed plankton samples. J. Cons. 25:29-35.

FROLANDER, H. F., AND I. PRATT.
1962. A bottom skimmer. Limnol. Oceanogr. 7:104-106.

HESTHAGEN, I. H.
1970. On the near-bottom plankton and benthic invertebrate fauna of the Josephine Seamount and the Great Meteor Seamount. METEOR Forschungsergeb., Reihe D. 8:61-70.

MACER, C. T.
1967. A new bottom-plankton sampler. J. Cons. 31:158-163.

PEARCY, W. G.
1970. Vertical migration of the ocean pink shrimp *Pandalus jordani*: A feeding and dispersal mechanism. Calif. Fish Game 56:125-129.
1972. Distribution and diel changes in the behavior of pink shrimp, *Pandalus jordani*, off Oregon. Proc. Natl. Shellfish. Assoc. 62:15-20.

ROBINSON, J. G.
In press. The vertical distribution and diel migration of pink shrimp (*Pandalus jordani*) off Oregon. Oreg. Fish Comm. Invest. Rep.

RUSSELL, F. S.
1928. A net for catching plankton near the bottom. J. Mar. Biol. Assoc. U.K. 15:105-108.

TEGELBERG, H. C., AND J. M. SMITH.
1957. Observations on the distribution and biology of the pink shrimp (*Pandalus jordani*) off the Washington coast. Wash. Dep. Fish., Fish. Res. Pap. 2(1):25-35.

WICKSTEAD, J.
1953. A new apparatus for the collection of bottom plankton. J. Mar. Biol. Assoc. U.K. 32:347-355.

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HARNESS FOR ATTACHMENT OF AN ULTRASONIC TRANSMITTER TO THE RED DRUM, *SCIAENOPS OCELLATA*

The use of small ultrasonic transmitters for studying the movement and behavior of fish in the field is becoming very popular (Stasko 1971). As a result various methods have been devised for attaching transmitters to fish either externally or internally. These methods involve hooking into the dorsal musculature or insertion into the stomach (Henderson et al. 1966), surgical implantation into the peritoneal cavity (Hart and Summerfelt 1975), and others (Ohsumi 1969). The suitability of a procedure is dependent on the species of fish and on the particular objective of the study. For studies we are initiating on movements of the red drum, *Sciaenops ocellata*, none of the existent procedures were found to be entirely satisfactory.

This note describes a simple inelastic harness we have developed for the external attachment of an ultrasonic transmitter to the caudal peduncle. This attachment method is markedly superior to other methods we have tried with the red drum. We believe this procedure will be of immediate value to many workers involved in tracking studies and therefore we are describing it now rather than awaiting the completion of our investigation of migratory movements of the red drum.

Materials and Methods

The inelastic harness for attaching an ultrasonic transmitter to the caudal peduncle is shown in Figure 1. The components of the harness are as follows:

1. An inelastic plastic pull-tie (5 × 190 mm) of sufficient length to encircle the caudal peduncle;
2. Sections of soft Tygon[1] tubing (6-mm OD) and soft rubber tubing (12-mm OD, 1.5-mm wall thickness) threaded over the pull-tie to provide a soft flat cushion that minimizes abrasions and chafing to the fish when the pull-tie is attached and tightened;
3. Small plastic pull-ties to firmly affix the transmitter to the large pull-tie and tubing described above.

When attaching the harness, the large pull-tie is tightened just enough such that it fits snugly around the caudal peduncle and cannot slip over the tail (Figure 1 inset). Care must be taken not to tighten the tie so tightly that it compresses the peduncle. If the latter occurs, the tie must be cut off with scissors and replaced. These ties can only be tightened. The final position of the transmitter itself should be on the dorsal surface of the peduncle with the axis of the transmitter situated at a right angle to the longitudinal axis of the fish. After attachment the overlapping section of the pull-tie is cut off.

Harnesses are preconstructed prior to the time of use such that in the field the only modifications required are the addition or removal of small sections of Tygon and rubber tubing to provide a cushion of the exact size for a particular fish. A preconstructed harness can be attached to a red drum in less than 5 min. Plastic pull-ties of various lengths and widths are available at most hardware stores that stock materials used by electricians.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

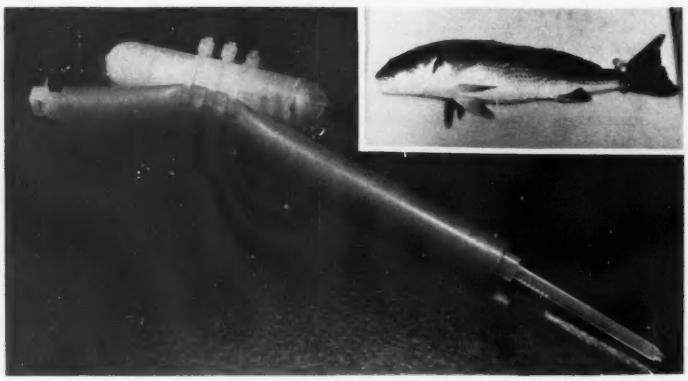

FIGURE 1.—Inelastic harness for attachment of ultrasonic transmitter to caudal peduncle of red drum. Transmitter = Smith Root SR 69. Total length of harness = 190 mm. Inset: Red drum (3.2 kg) with harness and transmitter attached.

The red drum used for testing the harness were caught in the Matanzas Inlet, Fla., by hook and line and maintained in captivity for approximately 2 mo prior to testing.

Results and Discussion

Observations of the suitability of the inelastic harness were conducted in a 3.3-m diameter fiber glass tank, in an enclosed half-acre pond (max depth 2.5 m), and in the Intracoastal Waterway near the Whitney Marine Laboratory. In the fiber glass tank, two red drum (2.5, 3.5 kg) with harnesses and "dummy" transmitters attached swam normally as soon as released and accepted food of shrimp and mullet within 30 min. A third red drum (ca. 3 kg) with harness and active transmitter (Smith Root SR 69) attached was released in the half-acre pond. During the 3-wk lifetime of the batteries in the transmitter, the movements of the fish were monitored almost daily with a receiver and hydrophone. The red drum moved actively about the pond, ate readily, and schooled with other fish. Mangrove roots, pilings, and other obstacles in the pond were not snagged by either the harness or the transmitter. More than 2 mo after the fish was initially released, the harness and inactive transmitter remained in place, and the fish continued to feed and behave normally.

A fourth red drum (3.2 kg) with harness and active transmitter attached was released into the Intracoastal Waterway on 12 January 1976 and tracked continuously for 7 h from a boat with a 74-kHz receiver and hydrophone. The position of the fish with respect to charted channel markers was recorded frequently to provide the summary described below. During the first 1.5 h after release, the fish moved approximately 1.6 km to the south of the release point. This movement was against the direction of the tidal flow. During the remaining time the fish moved 1.2 km to the north, again against the direction of the tidal flow. During this excursion, the fish entered the mouth of almost every creek encountered. At nightfall the fish had moved into a deep hole approximately 140 m up a small creek situated 400 m from the original release point. The fish was not located on the second day but on the third day was located at the edge of the main channel of the Intracoastal Waterway approximately 2 km to the south of the release point. Tracking of the fish had to be discontinued due to a malfunction in the receiver.

For the studies we are initiating on migratory movements of the red drum, the method selected for the attachment of the transmitter was extremely important, and we spent considerable time trying alternative methods. These methods included the hooking of saddles into either the dorsal or ventral musculature, surgical attachment to the pectoral girdle or to the lower jaw bone, surgical implantation into the peritoneal cavity, and insertion into the stomach. Utilization of the inelastic harness provided the following advantages over the other methods we tried.

1. The attachment procedure is simple and quick enough such that only a few minutes elapse between the time the fish is caught, tagged, and released.
2. The procedure results in no bleeding and causes minimal trauma, damage, or weakening of the fish.
3. The attachment is secure and assures that the transmitter remains attached to the red drum for the lifetime of the transmitters we are using (Smith Root SR 69 and SR 69A, lifetimes of 20 and 45 days).

Ichihara (1971) described a "saddle type" method for affixing a transmitter to a fish. This method employed an elastic strap of neoprene rubber that encircled the fish anterior to the dorsal fin. The author noted that fish with elastic harnesses of the saddle type died within 9 to 30 days. Regarding the above observations, we have also found that rubber elastic harnesses encircling the caudal peduncle are unsatisfactory because they constantly compress the peduncle and result in a progressive deterioration of the entire tail region. However, our inelastic harness causes no such deleterious effects. Although we have experimented with the inelastic harness on the red drum only, we are certain that it can be used with any large fish having a fairly rigid tail that is markedly broader than the caudal peduncle.

Acknowledgments

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Literature Cited

HART, L. G., AND R. C. SUMMERFELT.
1975. Surgical procedures for implanting ultrasonic transmitters into flathead catfish (*Pylodictis olivaris*). Trans. Am. Fish. Soc. 104:56-59.

HENDERSON, H. F., A. D. HASLER, AND G. G. CHIPMAN.
1966. An ultrasonic transmitter for use in studies of movements of fishes. Trans. Am. Fish. Soc. 95:350-356.

ICHIHARA, T.
1971. Ultrasonic, radio tags and various problems in fixing them to marine animal body. Suisancho. Suisan Kenkyusho Gyogyo Shigen Kenkyu Kaigido. 12:29-44 (Translated by Transl. Bur., Foreign Lang. Div., Fish. Res. Board Can., St. Andrews, N.B., Transl. 1981, 38 p.)

OHSUMI, S.
1969. How to attach the telemetry equipment to marine life. Kaiyoseibutsu Telem. Kenkyu Kaiho 2:32-36. Translated by Transl. Bur., Foreign Lang. Div., Fish. Res. Board Can., St. Andrews, N.B., Transl. 1929, 11 p.)

STRASKO, A. B.
1971. Review of field studies on fish orientation. Ann. N.Y. Acad. Sci. 188:12-29.

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INDEX

Fishery Bulletin Vol. 74, No. 1-4, 1976

ABLE, K. W., and J. A. MUSICK, "Life history, ecology, and behavior of *Liparis inquilinus* (Pisces: Cyclopteridae) associated with the sea scallop, *Placopecten magellanicus*" 409

"Abundance of macrocrustaceans in a natural marsh and a marsh altered by dredging, bulkheading, and filling," by Lee Trent, Edward J. Pullen, and Raphael Proctor 195

ACKER, WILLIAM C.–see LORD et al.

"(An) acoustic method for the high-seas assessment of migrating salmon," by Gary Lord, William C. Acker, Allan C. Hartt, and Brian J. Rothschild 104

Actiniaria
  continental shelf and slope, U.S. east coast
    Actinauge verrilli 872
    Actinostola callosa 865
    Amphianthus nitidus 873
    Antholoba perdix 869
    Bolocera tuediae 863
    Edwardsia sulcata 860
    Halcampa duodecimcirrata 862
    Haliplanella luciae 870
    Haloclava producta 863
    Hormathia nodosa 871
    Hormathia nodosa(?) 872
    Metridium senile fimbriatum 870
    Paranthus rapiformis 868
    Peachia parasitica 863
    Phelliactis americana 872
    Sagartiogeton verrilli 870
    Stephanauge nexilis 875
    Stephanauge(?) *spongicola* 875
    Stomphia coccinea 868
    Tealia crassicornis 865

"Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae," by Paul Struhsaker and James H. Uchiyama 9

Age determination
  butterflyfish, tropical reef
    otoliths, daily growth rings 990
  larval and adult fishes
    daily growth increments in otoliths 1
  nehu, Hawaiian Islands
    daily growth increments of sagittae 9

"Age determination of a tropical reef butterflyfish utilizing daily growth rings of otoliths," by Stephen Ralston 990

AHLSTROM, ELBERT H.–see BUTLER and AHLSTROM

Alaska, southeastern
  Sashin Creek
    salmon, coho, life history 897

Albacore–see Tuna, albacore

Alopias superciliosus–see Shark, bigeye thresher

Alosa sapidissima–see Shad, American

ALVAREZ, JOSE, CHRIS O. ANDREW, and FRED J. PROCHASKA, "Dual structural equilibrium in the Florida shrimp processing industry" 879

"Analysis of returns of tagged Gulf menhaden," by Paul J. Pristas, Eldon J. Levi, and Robert L. Dryfoos 112

Anchovy, northern
  ^{14}C-benzene
    uptake, distribution, and depuration 545
  California Current
    larvae, food and feeding 517
  fishery, development, and example application of simulation model 118
  growth of laboratory-reared in Southern California
    comparisons 277
    growth curve 274
    hatching to juvenile 272
    juvenile to adult 273
    weight-length relation 276
  larvae, culture and growth
    laboratory cultured foods 81
    survival at metamorphosis 85
  swim bladder inflation, diel changes
    adaptive advantages 854
    diel rhythm 849
    larval length 850
    mechanism 852
    relation between sinking speed, swim bladder volume, and larval length 850
    vertical migration 853
  thermal tolerance and resistance
    development and growth 440
    embryos and larvae 435
    juveniles and adults 434

ANDREW, CHRIS O.–see ALVAREZ et al.

Anoplopoma fimbria–see Sablefish

Apalachicola Bay, Florida
  epibenthic fish and invertebrate populations
    long-term fluctuations 311

"(The) application of systematic sampling to a study of infauna variation in a soft substrate environment," by Stephen Scherba, Jr. and Vincent F. Gallucci 937

ARTHUR DAVID K., "Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*" 517

"Aspects of the reproductive biology of the weakfish,

Cynoscion regalis (Sciaenidae), in North Carolina," by John V. Merriner 18

Atlantic, North
calanoid copepods
caloric values of some 218

Atlantic, western North
bigeye thresher shark, observations on 221
fishing effort estimation from aerial search data... 503

Atlantic Ocean
seatrouts
protein taxonomy 599

Auke Creek, Alaska
salmon, pink
production of fry and adults from gravel incubators and natural spawning 961

BAILEY, JACK E., JEROME J. PELLA, and SIDNEY G. TAYLOR, "Production of fry and adults of the 1972 brood of pink salmon, *Oncorhynchus gorbuscha*, from gravel incubators and natural spawning at Auke Creek, Alaska" 961

Barnacles, goose
La Jolla, California
on beached flotsam 212

Bass, striped
^{14}C-benzene
uptake, distribution, and depuration 545
benzene effects of
caloric content 694
fat content 694
growth 694

Bathynectes superbus
epizoites associated with 225

BELL, JONATHAN–see HANSON and BELL

BENVILLE, PETE, JR.–see KORN et al.

Benzene
bass, striped
effects on growth, fat content, and caloric content . 694

"Biology of five species of searobins (Pisces, Triglidae) from the northeastern Gulf of Mexico," by Thomas C. Lewis and Ralph W. Yerger 93

BISSON, PETER A., and GERALD E. DAVIS, "Production of juvenile chinook salmon, *Oncorhynchus tshawytscha*, in a heated model stream." 763

Bivalve variation
application of systematic sampling to study of, in soft substrate environment..... 944

BLACKBURN, MAURICE, and WALTER NELLEN, "Distribution and ecology of pelagic fishes studied from eggs and larvae in an upwelling area off Spanish Sahara" 885

BOND, CARL E.–see CRONE and BOND

BRAY, RICHARD N.–see EBELING and BRAY

BREDER, CHARLES M., JR., "Fish schools as operational structures" 471

Brevoortia patronus–see Menhaden, Gulf

Brevoortia tyrannus–see Menhaden, Atlantic

BREWER, GARY D., "Thermal tolerance and resistance and resistance of the northern anchovy, *Engraulis mordax*" 433

BRINTON, EDWARD, "Population biology of *Euphausia pacifica* off southern California" 733

Bristol Bay, Alaska
salmon, sockeye
foods of juvenile in inshore coastal waters, 1966-67. 458

BROTHERS, EDWARD B., CHROSTOPHER P. MATHEWS, AND REUBEN LASKER, "Daily growth increments in otoliths from larval and adult fishes"..... 1

BROWN, JOHN C.–see HEWITT et al.

BRUSHER, HAROLD A., and LARRY H. OGREN, "Distribution, abundance, and size of penaeid shrimps in the St. Andrew Bay system, Florida"..... 158

Buoy, acoustic
used for high-seas assessment of migrating salmon.. 104

BUTLER, JOHN L., and ELBERT H. AHLSTROM, "Review of the deep-sea fish genus *Scopelengys* (Neoscopelidae) with a description of a new species *Scopelengys clarkei*, from the central Pacific" 142

Butterflyfish, millet-seed
age determination using daily growth rings of otoliths 990

CAILLOUET, CHARLES W.–see LANSFORD et al.

California, southern
DDT and metabolites in sediments off..... 27
Euphausia pacifica
population biology..... 733

California Current
sonar mapping
development and use for pelagic stock assessment . 281

California Current, central region
zooplankton and euphausiid populations
density, vertical range, and diel movement..... 925

Callinectes sapidus–see Crab, blue

"Caloric values of some North Atlantic calanoid copepods," by Geoffrey C. Laurence..... 218

Cancer irroratus–see Crab, rock

Cancer magister–see Crab, Dungeness

CARLSON, H. RICHARD, "Foods of juvenile sockeye salmon, *Oncorhynchus nerka*, in the inshore coastal waters of Bristol Bay, Alaska, 1966-67"..... 458

CARR, WILLIAM E. S., and THOMAS B. CHANEY, "Harness for attachment of an ultrasonic transmitter to the red drum, *Sciaenops ocellata*" 998

CASEY, JOHN G.–see STILLWELL and CASEY

Ceriantharia
continental shelf and slope, U.S. east coast

Ceriantheopsis americanus 858
Cerianthus borealis 857

"Ceriantharia, Zoanthidea, Corallimorpharia, and Actiniaria from the continental shelf and slope off the eastern coast of the United States," by Bernt Widersten 857

Chaetodon miliaris–see Butterflyfish, millet-seed

CHANEY, THOMAS B.–see CARR and CHANEY

CHENG, LANNA, and RALPH A. LEWIN, "Goose barnacles (Cirripedia: Thoracica) on flotsam beached at La Jolla, California" 212

Chesapeake Bight
galatheid crustaceans
occurrence of two in 462

CHESS, JAMES R.–see HOBSON and CHESS

CHITTENDEN, MARK E., JR., "Present and historical spawning grounds and nurseries of American shad, *Alosa sapidissima*, in the Delaware River" 343

_____, "Weight loss, mortality, feeding, and duration of residence of adult American shad, *Alosa sapidissima*, in fresh water" 151

Citharichthys sordidus–see Sanddab, Pacific

CLARKE, THOMAS A., and PATRICIA J. WAGNER, "Vertical distribution and other aspects of the ecology of certain mesopelagic fishes taken near Hawaii" 635

Clupea harengus pallasi–see Herring, Pacific

COE, JAMES M.–see PERRIN et al.

COLLINS, JEFF, "Oil and grease: A proposed analytical method for fishery waste effluents" 681

_____, and RICHARD D. TENNY, "Fishery waste effluents: A method to determine relationships between chemical oxygen demand and residue" 725

"Comparison of the most successful and least successful west coast albacore troll fishermen," by Donald F. Keene and William G. Pearcy 973

"Contribution of the net plankton and nannoplankton to the standing stocks and primary productivity in Monterey Bay, California during the upwelling season," by David L. Garrison 183

Copepods, calanoid
North Atlantic Ocean
caloric values of some 218

Corallimorpharia
continental shelf and slope, U.S. east coast
Corynactis delawarei 858

Cottus aleuticus
populations of sympatric in four adjacent salmon-producing coastal streams on Vancouver Island 131

Cottus asper
populations of sympatric in four adjacent salmon-producing coastal streams on Vancouver Island 131

Crab
North American fisheries regulations and their rationales
procedures for changing laws and regulations 630

Crab, blue
east coast
fishery regulations and their rationales 628
West Bay, Texas
abundance in natural and altered marshes 195

Crab, Dungeness
eggs
mortalities and epibiotic fouling of, from wild populations 201
larval dynamics off central Oregon coast, 1970-71
abundance 357
climate 357
distribution 357
gut-fullness analysis 364
hydrographic features 353
population analyses, larval 359
sampling variability 356
west coast
fishery regulations and their rationales 626

Crab, fiddler
mercury, cadmium, and lead salts
regeneration and ecdysis, effects on 464

Crab, king
Alaska
fishery regulations and their rationales 624

Crab, rock
size composition and growth of young in Maine
growth 952
sex ratio 951
size composition and seasonal distribution 949

Crab, snow
Alaska
fishery regulations and their rationales 625
eastern Canada
fishery regulations and their rationales 627
electrophoretic evidence of hybrid 693

Crab, stone
Florida
fishery regulations and their rationales 630

Crab fisheries
regulations and their rationales
Alaska king 624
Alaska snow 625
blue, east coast 628
Canada, eastern snow 627
Dungeness, west coast 626
Florida stone 630

CRADDOCK, DONOVAN R., "Effects of increased water temperature on *Daphnia pulex*" 403

Crassostrea gigas–see Oyster, Pacific

CRAWFORD, L., and M. J. KRETSCH, "Effects of cooking in air or in nitrogen on the development of fishy flavor

in the breast meat of turkeys fed tuna oil with and without α-tocopherol supplement or injection"..... 89

Croaker, white
seasonal spawning cycle 983

CRONE, RICHARD A., and CARL E. BOND, "Life history of coho salmon, *Oncorhynchus kisutch*, in Sashin Creek, southeastern Alaska" 897

Crustaceans
restraining living planktonic 220

"Culture and growth of northern anchovy, *Engraulis mordax*, larvae," by John R. Hunter 81

Cynsocion macdonaldi–see Totoaba

Cynoscion regalis–see Weakfish

DDD
in sediments off southern California..... 27

DDE
in sediments off southern California..... 27

DDT
and metabolites in sediments off southern California. 27

"DDT and its metabolites in the sediments off southern California," by John S. MacGregor 27

"Daily growth increments in otoliths from larval and adult fishes," by Edward B. Brothers, Christopher P. Mathews, and Reuben Lasker 1

Daphnia pulex
water temperature, effects of increased
discharges of heated water..... 405
water passing through cooling systems..... 406

DAVIS, GERALD E.–see BISSON and DAVIS

"Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California," by Alfred W. Ebeling and Richard N. Bray..... 703

Decision theory
salmon fishery
data acquisition and management 837

"Decision theory applied to the simulated data acquisition and management of a salmon fishery," by Gary E. Lord..... 837

Delaware River
shad, American
present and historical spawning grounds and nurseries..... 343

"Description of zoeae of coonstripe shrimp, *Pandalus hypsinotus*, reared in the laboratory," by Evan Haynes 323

"Development and example application of a simulation model of the northern anchovy fishery," by Michael F. Tillman and Donald Stadelman..... 118

"Development and use of sonar mapping for pelagic stock assessment in the California Current area," by Roger P. Hewitt, Paul E. Smith, and John C. Brown..... 281

Diatoms
freshwater and estuarine, benthic
menhaden, Atlantic, grazing by adult 689

"Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax*," by John R. Hunter and Carol Sanchez..... 847

"Distribution, abundance, and size of penaeid shrimps in the St. Andrew Bay system, Florida," by Harold A. Brusher and Larry H. Ogren 158

"Distribution and ecology of pelagic fishes studied from eggs and larvae in an upwelling area off Spanish Sahara," by Maurice Blackburn and Walter Nellen 885

"Distribution, food, and feeding of the threespine stickleback, *Gasterosteus aculeatus*, in Great Central Lake, Vancouver Island, with comments on competition for food with juvenile sockeye salmon, *Oncorhynchus nerka*," by J. I. Manzer..... 647

DOTSON, RONALD C., "Minimum swimming speed of albacore, *Thunnus alalunga*"..... 955

Drum, red
ultrasonic transmitter, harness for attachment of ... 998

DRYFOOS, ROBERT L.–see PRISTAS et al.

"Dual structural equilibrium in the Florida shrimp processing industry," by Jose Alvarez, Chris O. Andrew, and Fred J. Prochaska..... 879

EBELING, ALFRED W., and RICHARD N. BRAY, "Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California"..... 703

"Ecology of Hawaiian sergestid shrimps (Penaeidea: Sergestidae)," by John F. Walters..... 799

"Economic and financial analysis of increasing costs in the Gulf shrimp fleet," by Wade L. Griffin, Newton J. Wardlaw, and John P. Nichols..... 301

EDGAR, ROBERT K., and JAMES G. HOFF, "Grazing of freshwater and estuarine, benthic diatoms by adult Atlantic menhaden, *Brevoortia tyrannus*"..... 689

"Effects of benzene on growth, fat content, and caloric content of striped bass, *Morone saxatilis*," by Sid Korn, Jeannette W. Struhsaker, and Pete Benville, Jr..... 694

"Effects of cooking in air or in nitrogen on the development of fishy flavor in the breast meat of turkeys fed tuna oil with and without α-tocopherol supplement or injection," by L. Crawford and M. J. Kretsch 89

"Effects of increased water temperature on *Daphnia pulex*," by Donovan R. Craddock..... 403

"Effects of mercury, cadmium, and lead salts on regeneration and ecdysis in the fiddler crab, *Uca pugilator*," by Judith S. Weis 464

"Effects of temperature and salinity on the survival of winter flounder embryos," by Carolyn A. Rogers..... 52

Effluents – see Fishery waste effluents

Eggs, fish–see Fish eggs

"Electrophoretic evidence of hybrid snow crab, *Chionocetes bairdi* × *opilio*," by Allyn G. Johnson 693

"(An) energetics model for the exploited yellowfin tuna, *Thunnus albacares*, population in the eastern Pacific Ocean," by Gary D. Sharp and Robert C. Francis 36

Engraulis mordax–see Anchovy, northern

Eopsetta jordani–see Sole, petrale

"(An) epibenthic sampler used to study the ontogeny of vertical migration of *Pandalus jordani* (Decapoda, Caridea)," by Peter C. Rothlisberg and William G. Pearcy 994

Epizoites
  associated with *Bathynectes superbus* 225

"Epizoites associated with *Bathynectes superbus* (Decapoda: Portunidae)," by Elizabeth G. Lewis. 225

"Estimates of rates of tag shedding by North Pacific albacore, *Thunnus alalunga*," by R. Michael Laurs, William H. Lenarz, and Robert N. Nishimoto. 675

"Estimation of fishing effort in the western North Atlantic from aerial search data," by M. L. Parrack 503

Euphausia pacifica
  population biology off southern California
    annual biomass 752
    growth 745
    recruitment efficiency and spatial aggregation of eggs 743
    sex ratio 755
    southern California eddy 736
    spawning and recruitment 738
    survivorship 749
    temperature relationships of spawners and larvae . 744

Euphausiids
  California Current, central region
    density, vertical range, and diel movement. 925

Euthynnus lineatus–see Skipjack, black

"Feeding behavior, food consumption, growth, and respiration of the squid *Loligo opalescens* raised in the laboratory," by Ann C. Hurley 176

"Fertilization method quantifying gamete concentrations and maximizing larvae production in *Crassostrea gigas*," by William H. Staeger and Howard F. Horton .. 698

"First record of the melon-headed whale, *Peponocephala electra*, in the eastern Pacific, with a summary of world distribution," by William F. Perrin 457

Fish, adult
  daily growth increments in otoliths 1

Fish, epibenthic
  long-term fluctuations of populations in Apalachicola Bay, Florida
    distribution. 313
    physicochemical parameters 313
    seasonal fluctuations of dominant species 314

Fish, mesopelagic
  vertical distribution and other aspects of ecology near Hawaii
    avoidance 643
    migration 641
    sex ratio 643
    sexual dimorphism 643

Fish, pelagic
  eggs and larvae, distribution and ecology off Spanish Sahara
    anchovy eggs, spatial and temporal distributions .. 893
    identification and enumeration 888
    sardine eggs, spatial and temporal distributions... 893
    spatial distribution 891
    temperature and chlorophyll *a* 888
    zooplankton 886

Fish, trophic interactions
  activity patterns of planktivorous fishes 580
  collecting fishes 570
  collecting zooplankters. 569
  fishes studied 568
  zooplankter activity patterns 571
  zooplankter volumes 571

Fish catches
  gill nets
    relation to frontal periods 449

Fish eggs
  Spanish Sahara
    distribution and ecology of pelagic in an upwelling area off. 885

Fish fauna
  associated with offshore platforms in northeastern Gulf of Mexico
    comparison of two platforms 395
    faunal composition 389
    habitat occupation and activity patterns. 396
    winter-summer contrast 395

Fish larvae
  anchovy, northern
    diel changes in swim bladder inflation 847
  California Current
    anchovy, northern 517
    mackerel, jack 517
    sardine, Pacific. 517
  daily growth increments in otoliths 1
  herring, Pacific
    predator-prey relationship between, and *Hyperoche medusarum* 669
    northern anchovy, culture and growth 81
  Spanish Sahara
    distribution and ecology of pelagic in an upwelling area off. 885

Fish schools
  as operational structures
    geometrical models. 472
    locomotor problems. 491
    movements 482
    shape 482
    size 482
    spacing 476

traffic problems 486
turning problems 484

"Fish schools as operational structures," by Charles M. Breder, Jr. 471

FISHER, WILLIAM S., and DANIEL E. WICKHAM, "Mortalities and epibiotic fouling of eggs from wild populations of the Dungeness crab, *Cancer magister*" .. 201

Fishery waste effluents
chemical oxygen demand and residue
method to determine relationships between 725
oil and grease
proposed analytical method 681

"Fishery waste effluents: A method to determine relationships between chemical oxygen demand and residue," by Jeff Collins and Richard D. Tenny 725

Fishes, reef
Santa Barbara, California
day versus night activity in a kelp forest 703

Fishing effort estimation
Atlantic, western north
aerial search data 503

FLANAGAN, CHRISTINE A., and JOHN R. HENDRICKSON, "Observations on the commercial fishery and reproductive biology of the totoaba, *Cynoscion macdonaldi*, in the northern Gulf of California" 531

Flatfish
Oregon, continental shelf
food of five species of cooccurring 984

Florida
shrimp processing industry
dual structural equilibrium 880

Flounder, winter
embryos, effects of temperature and salinity on survival
embryonic development 56
incubation time and duration of hatching interval . 55
influence on total and viable hatch 53

"Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*," by David K. Arthur 517

"Food of five species of cooccurring flatfishes on Oregon's continental shelf," by Michael Kravitz 984

"Foods of juvenile sockeye salmon, *Oncorhynchus nerka*, in the inshore coastal waters of Bristol Bay, Alaska, 1966-67," by H. Richard Carlson 458

FRANCIS, ROBERT C.–see SHARP and FRANCIS

Frontal periods
relation of fish catches in gill nets to 449

FUIMAN, LEE A., "Notes on the early development of the sea raven, *Hemitripterus americanus*" 467

"Further observations of the feeding ecology of postlarval pinfish, *Lagodon rhomboides*, and spot, *Leiostomus xanthurus*," by Martin A. Kjelson and George N. Johnson 423

GADBOIS, D. F., E. M. RAVESI, and R. C. LUNDSTROM, "Occurrence of volatile N-nitrosamines in Japanese salmon roe" 683

GALLUCCI, VINCENT F.–see SCHERBA and GALLUCCI

GARRISON, DAVID L., "Contribution of the net plankton and nannoplankton to the standing stocks and primary productivity in Monterey Bay, California during the upwelling season" 183

Gasterosteus aculeatus–see Stickleback, threespine

GAUGLITZ, ERICH J., JR.–see HALL et al.

Genyonemus lineatus–see Croaker, white

Glyptocephalus zachirus–see Sole, rex

GOLDBERG, STEPHEN R., "Seasonal spawning cycles of the sciaenid fishes *Genyonemus lineatus* and *Seriphus politus*" 983

"Goose barnacles (Cirripedia: Thoracica) on flotsam beached at La Jolla, California," by Lanna Cheng and Ralph A. Lewin 212

"Grazing of freshwater and estuarine, benthic diatoms by adult Atlantic menhaden, *Brevoortia tyrannus*," by Robert K. Edgar and James G. Hoff 689

Great Central Lake, Vancouver Island
threespine stickleback
distribution, food, and feeding 647
food, with juvenile sockeye salmon, competition for 647

GRIFFIN, WADE L., NEWTON J. WARDLAW, and JOHN P. NICHOLS, "Economic and financial analysis of increasing costs in the Gulf shrimp fleet" 301

Growth
daily increments in otoliths
larval and adult fishes 1
daily increments of sagittae
nehu, Hawaiian Islands 9

"Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific," by William F. Perrin, James M. Coe, and James R. Zweifel 229

Growth model
fish, prehatch and posthatch 609

"Growth of laboratory-reared northern anchovy, *Engraulis mordax*, from southern California," by Gary T. Sakagawa and Makoto Kimura 271

Gulf of California, northern
totoaba
commercial fishery and reproductive biology 531

Gulf of Mexico
seatrouts
protein taxonomy 599
shrimp fleet
increasing costs, economic and financial analysis of 301

Gulf of Mexico, northeastern
fish fauna
observations on, associated with offshore platforms 387
searobins
biology of five species 93

Gulf of Mexico, northern
Gulf menhaden
analysis of returns of tagged 112

HAEFNER, PAUL A., JR.–see LAIRD et al.

Halibut, Pacific
Pacific Ocean, northeast
mercury content 783

HALL, ALICE S., FUAD M. TEENY, and ERICH J. GAUGLITZ, JR., "Mercury in fish and shellfish of the northeast Pacific. II. Sablefish, *Anoplopoma fimbria*" 791

———, ———, LAURA G. LEWIS, WILLIAM H. HARDMAN, and ERICH J. GAUGLITZ, JR., "Mercury in fish and shellfish of the northeast Pacific. I. Pacific halibut, *Hippoglossus stenolepis*" 783

HANSON, CHARLES H., and JONATHAN BELL, "Subtidal and intertidal marine fouling on artificial substrata in northern Puget Sound, Washington" 377

HARDMAN, WILLIAM H.–see HALL et al.

"Harness for attachment of an ultrasonic transmitter to the red drum, *Sciaenops ocellata*," by William E. Carr and Thomas B. Chaney 998

HARRELL, LEE W., ANTHONY J. NOVOTNY, MICHAEL H. SCHIEWE, and HAROLD O. HODGINS, "Isolation and description of two vibrios pathogenic to Pacific salmon in Puget Sound, Washington" 447

HART, ALLAN C.–see LORD ET AL.

HASTINGS, ROBERT W., LARRY H. OGREN, and MICHAEL T. MABRY, "Observations on the fish fauna associated with offshore platforms in the northeastern Gulf of Mexico" 387

HAURY, LOREN R., "Method for restraining living planktonic crustaceans" 220

Hawaii
mesopelagic fishes taken near
vertical distribution and other aspects of ecology 635
sergestid shrimps, ecology of 799

Hawaiian Islands
black skipjack, second record 207
nehu
age and growth as indicated by daily growth increments of sagittae 9

HAYNES, EVAN, "Description of zoeae of coonstripe shrimp, *Pandalus hypsinotus*, reared in the laboratory" 323

Hemitripterus americanus–see Sea raven

HENDRICKSON, JOHN R.–see FLANAGAN and HENDRICKSON

Herring, Pacific
predator-prey relationship between larvae and *Hyperoche medusarum* 669

HEWITT, ROGER P., PAUL E. SMITH, and JOHN C. BROWN, "Development and use of sonar mapping for pelagic stock assessment in the California Current area" 281

Hippoglossus stenolepis–see Halibut, Pacific

HIRSCH, NINA–see KORN et al.

HOBSON, EDMUND S., and JAMES R. CHESS, "Tropic interactions among fishes and zooplankters near shore at Santa Catalina Island, California" 567

HODGINS, HAROLD O.–see HARRELL et al.

HOFF, JAMES G.–see EDGAR and HOFF

Homarus americanus–see Lobster, American

HORTON, HOWARD F.–see STAEGER and HORTON

HUNTER, JOHN R., "Culture and growth of northern anchovy, *Engraulis mordax*, larvae" 81

———, and CAROL SANCHEZ, "Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax*" 847

HURLEY, ANN C., "Feeding behavior, food consumption, growth, and respiration of the squid *Loligo opalescens* raised in the laboratory" 176

Hyperoche medusarum
Pacific herring larvae
predator-prey relationship between 669

"Incidence of cull lobsters, *Homarus americanus*, in commercial and research catches off the Maine coast," by Jay S. Krouse 719

Infauna variation
soft substrate environment
application of systematic sampling to study of 937

Invertebrates, epibenthic
long-term fluctuations of populations in Apalachicola Bay, Florida
distribution 313
dominant species, seasonal fluctuations of 314
physicochemical parameters 313

"Isolation and description of two vibrios pathogenic to Pacific salmon in Puget Sound, Washington," by Lee W. Harrell, Anthony J. Novotny, Michael H. Schiewe, and Harold O. Hodgins 447

Japan
salmon roe
N-nitrosamines, occurrence of volatile 683

JOHNSON, ALLYN G., "Electrophoretic evidence of hybrid snow crab, *Chionoecetes bairdi* × *opilio*" 693

JOHNSON, GEORGE N.–see KJELSON and JOHNSON

Katsuwonus pelamis–see Tuna, skipjack

KEENE, DONALD F., and WILLIAM G. PEARCY, "Comparison of the most successful west coast albacore troll fishermen" 973

Kelp
Santa Barbara, California
reef fishes, day versus night activity 703

KIMURA, MAKOTO–see SAKAGAWA and KIMURA

KJELSON, MARTIN A., and GEORGE N. JOHNSON, "Further observations of the feeding ecology of postlarval pinfish, *Lagodon rhomboides*, and spot, *Leiostomus xanthurus*" 423

KOBYLINSKI, GERARD J.–see LIVINGSTON et al.

KORN, SID, NINA HIRSCH, and JEANNETTE W. STRUHSAKER, "Uptake, distribution, and depuration of ^{14}C-benzene in northern anchovy, *Engraulis mordax*, and striped bass, *Morone saxatilis*" 545

_____, JEANNETTE W. STRUHSAKER, and PETE BENVILLE, JR., "Effects of benzene on growth, fat content, and caloric content of striped bass, *Morone saxatilis*" 694

KRAVITZ, MICHAEL J., "Food of five species of cooccurring flatfish on Oregon's continental shelf" 984

KRETSCH, M. J.–see CRAWFORD and KRETSCH

KROUSE, JAY S., "Incidence of cull lobsters, *Homarus americanus*, in commercial and research catches off the Maine coast" 719

_____, "Size composition and growth of young rock crab, *Cancer irroratus*, on a rocky beach in Maine" 949

La Jolla, California
goose barnacles on flotsam beached at 212

Lagodon rhomboides–see Pinfish

LAIRD, CHAE E., ELIZABETH G. LEWIS, and PAUL A. HAEFNER, JR.

"Occurrence of two galatheid crustaceans, *Munida forceps* and *Munidopsis bermudezi*, in the Chesapeake Bight of the western North Atlantic Ocean" 462

LANSFORD, LAWRENCE M., CHARLES W. CAILLOUET, and KENNETH T. MARVIN, "Phosphoglucomutase polymorphism in two penaeid shrimps, *Penaeus brasiliensis* and *Penaeus aztecus subtilis*" 453

Larvae
crab, Dungeness
larval dynamics off central Oregon coast, 1970-71 .. 353

Larvae, fish–see Fish larvae

"Larval dynamics of the Dungeness crab, *Cancer magister*, off the central Oregon coast, 1970-71," by R. Gregory Lough 353

LASKER, REUBEN–see BROTHERS et al.

_____–see ZWEIFEL and LASKER

LAURENCE, GEOFFREY C., "Caloric values of some North Atlantic calanoid copepods" 218

LAURS, R. MICHAEL, WILLIAM H. LENARZ, and ROBERT N. NISHIMOTO, "Estimates of rates of tag shedding by North Pacific albacore, *Thunnus alalunga*" 675

Leiostomus xanthurus–see Spot

LENARZ, WILLIAM H.–see LAURS et al.

Lepidopsetta bilineata–see Sole, rock

LEVI, ELDON J.–see PRISTAS et al.

LEWIN, RALPH A.–see CHENG and LEWIN

LEWIS, ELIZABETH G., "Epizoites associated with *Bathynectes superbus* (Decapoda: Portunidae)" 225

_____–see LAIRD et al.

LEWIS, FRANK G., III–see LIVINGSTON et al.

LEWIS, LAURA G.–see HALL et al.

LEWIS, THOMAS C., and RALPH W. YERGER, "Biology of five species of searobins (Pisces, Triglidae) from the northeastern Gulf of Mexico" 93

"Life history, ecology, and behavior of *Liparis inquilinus* (Pisces: Cyclopteridae) associated with the sea scallop, *Placopecten magellanicus*," by K. W. Able and J. A. Musick 409

"Life history of coho salmon, *Oncorhynchus kisutch*, in Sashin Creek, southeastern Alaska," by Richard A. Crone and Carl E. Bond 897

Liparis inquilinus
life history, ecology, and behavior of, associated with sea scallop
abundance, geographic variation 418
behavior of 414
diel rhythm in fish-scallop association 416
feeding 414
juveniles 412
larvae 412
resting 413
spawning behavior 412

LIVINGSTON, ROBERT J., GERARD J. KOBYLINSKI, FRANK G. LEWIS, III, and PETER F. SHERIDAN, "Long-term fluctuations of epibenthic fish and invertebrate populations in Apalachicola Bay, Florida" 311

Lobster, American
culls off Main coast, incidence of
fishing intensity, effect on 721
seasonal and size variation in 719
value loss of catch due to 723

Loligo opalescens
raised in laboratory
feeding behavior, food consumption, growth, and respiration 176

"Long-term fluctuations of epibenthic fish and invertebrate populations in Apalachicola Bay, Florida," by Robert J. Livingston, Gerard J. Kobylinski, Frank G. Lewis, III, and Peter F. Sheridan 311

LORD, GARY E., "Decision theory applied to the simulated data acquisition and management of a salmon fishery" 837

_____, WILLIAM C. ACKER, ALLAN C. HARTT, and BRIAN J. ROTHSCHILD, "An acoustic method for the high-seas assessment of migrating salmon" 104

LOUGH, R. GREGORY, "Larval dynamics of the Dungeness crab, *Cancer magister*, off the central Oregon coast, 1970-71" 353

LUNDSTROM, R. C.–see GADBOIS et al.

MABRY, MICHAEL T.–see HASTINGS et al.

MacGREGOR, JOHN S., "DDT and its metabolites in the sediments off southern California" 27

MACHIDORI, S.–see MASON and MACHIDORI

Mackerel, jack
California Current
larvae, food and feeding 517

McMAHON, ROBERT S.–see ZIMMERMAN and McMAHON

Macrocrustaceans
abundance in natural and altered marshes
catch between areas, comparison of 197
day and night catches, comparison of 196
dissolved oxygen, catch related to 197

Macrozooplankton
standing stocks off Oregon, seasonal and inshore-offshore variations 70

Maine
crab, rock
size composition and growth of young 949
lobsters, cull
commercial and research catches 719

Makaira nigricans–see Marlin, blue

MANOOCH, CHARLES S., III, "Reproductive cycle, fecundity, and sex ratios of the red porgy, *Pagrus pagrus* (Pisces: Sparidae), in North Carolina" 775

MANZER, J. I., "Distribution, food, and feeding of the threespine stickleback, *Gasterosteus aculeatus*, in Great Central Lake, Vancouver Island, with comments on competition for food with juvenile sockeye salmon, *Oncorhynchus nerka*" 647

Marine fouling
subtidal and intertidal, on artificial substrata in Puget Sound, Washington
fouling colonization of construction materials 379
fouling organisms, seasonal distribution 381
fouling organisms, vertical distribution in subtidal zone 382
physicochemical environment 378

Marlin, blue
Pacific, central North
von Bertalanffy growth curves 553

Marlin, striped
Pacific, central North
von Bertalanffy growth curves 553

MARVIN, KENNETH T.–see LANSFORD et al.

MASON, J.C., "Some features of coho salmon, *Oncorhynchus kisutch*, fry emerging from simulated redds and concurrent changes in photobehavior" 167

_____, and S. MACHIDORI, "Populations of sympatric sculpins, *Cottus aleuticus* and *Cottus asper*, in four adjacent salmon-producing coastal streams on Vancouver Island, B.C." 131

MATHEWS, CHRISTOPHER P.–see BROTHERS et al.

MATSUMOTO, WALTER M., "Second record of black skipjack, *Euthynnus lineatus*, from the Hawaiian Islands" 207

MAY, NELSON, LEE TRENT, AND PAUL J. PRISTAS, "Relation of fish catches in gill nets to frontal periods". 449

Menhaden, Atlantic
grazing of freshwater and estuarine, benthic diatoms by adults 689

Menhaden, Gulf
analysis of returns of tagged
autumn releases and recoveries 116
fishing areas 112
recovering tags, methods of 113
tagging, methods of 112
spring releases and recoveries 114

Menidia menidia–see Silverside, Atlantic

"Mercury in fish and shellfish of the northeast Pacific. I. Pacific halibut, *Hippoglossus stenolepis*," by Alice S. Hall, Faud M. Teeny, Laura G. Lewis, William H. Hardman, and Erich J. Gauglitz, Jr. 783

"Mercury in fish and shellfish of the northeast Pacific. II. Sablefish, *Anoplopoma fimbria*," by Alice S. Hall, Faud M. Teeny, and Erich J. Gauglitz, Jr. 791

MERRINER, JOHN V., "Aspects of the reproductive biology of the weakfish, *Cynoscion regalis* (Sciaenidae), in North Carolina" 18

"Method for restraining living planktonic crustaceans," by Loren R. Haury 220

Micronekton
standing stocks off Oregon, seasonal and inshore-offshore variations 70

MILLER, R. J., "North American crab fisheries: Regulations and their rationales" 623

"Minimum swimming speed of albacore, *Thunnus alalunga*," by Ronald C. Dotson 955

Monterey Bay, California
net plankton and nannoplankton
standing stocks and primary productivity during upwelling season, contribution to 183

Morone saxatilis–see Bass, striped

"Mortalities and epibiotic fouling of eggs from wild populations of the Dungeness crab, *Cancer magister*," by William S. Fisher and Daniel E. Wickham 201

Munida forceps
Chesapeake Bight
occurrence in 462

Munidopsis bermudezi
Chesapeake Bight
occurrence in 462

MUSICK, J.A.–see ABLE and MUSICK

N-nitrosamines
volatile, occurrence of
salmon roe, Japanese 683

Nannoplankton
Monterey Bay, California
standing stocks and primary productivity during upwelling season, contribution to 183

Nehu
age and growth, Hawaiian Islands
geographical comparison of growth rates 16
indicated by daily growth increments of sagittae .. 9

NELLEN, WALTER–see BLACKBURN and NELLEN

Nematobrachion sp.
California Current, central region
density, vertical range, and diel movement..... 932

Nematoscelis sp.
California Current, central region
density, vertical range, and diel movement..... 932

Nets, gill
fish catches
relation to frontal periods..... 449

NICHOLS, JOHN P.–see GRIFFIN et al.

NISHIMOTO, ROBERT N.–see LAURS et al.

"North American crab fisheries: Regulations and their rationales," by R. J. Miller..... 623

North Carolina
porgy, red
reproductive cycle, fecundity, and sex ratios 775
weakfish, reproductive biology..... 18

"Notes on the early development of the sea raven, *Hemitripterus americanus*," by Lee A. Fuiman..... 467

NOVOTNY, ANTHONY J.–see HARRELL et al.

Observations on the bigeye thresher shark, *Alopias superciliosus*, in the western North Atlantic," by Charles E. Stillwell and John G. Casey 221

"Observations on the commercial fishery and reproductive biology of the totoaba, *Cynoscion macdonaldi*, in the northern Gulf of California," by Christine A. Flanagan and John R. Hendrickson 531

"Observations on the fish fauna associated with offshore platforms in the northeastern Gulf of Mexico," by Robert W. Hastings, Larry H. Ogren, and Michael T. Mabry... 387

"Occurrence of two galatheid crustaceans, *Munida forceps*, and *Munidopsis bermudezi*, in the Chesapeake Bight of the western North Atlantic Ocean," by Chae E. Laird, Elizabeth G. Lewis, and Paul A. Haefner, Jr..... 462

"Occurrence of volatile N-nitrosamines in Japanese salmon roe," by D. F. Gadbois, E. M. Ravesi, and R. C. Lundstrom 683

OGREN, LARRY H.–see BRUSHER and OGREN

_____–see HASTINGS et al.

Oil and grease
fishery waste effluents
proposed analytical method 681

"Oil and grease: A proposed analytical method for fishery waste effluents," by Jeff Collins 681

Oncorhynchus gorbuscha–see Salmon, pink

Oncorhynchus kisutch–see Salmon, coho

Oncorhynchus nerka–see Salmon, sockeye

Oncorhynchus tshawytscha–see Salmon, chinook

"Optical malformations induced by insecticides in embryos of the Atlantic silverside, *Menidia menidia*," by Judith S. Weis and Peddrick Weis..... 208

Oregon
crab, Dungeness
larval dynamics off central coast, 1970-71 353
micronekton and macrozooplankton
season and inshore-offshore variations in standing stocks..... 70

Otoliths
daily growth increments, larval and adult fishes 1

Oyster, Pacific
fertilization method quantifying gamete concentrations and maximizing larvae production 698

Pacific, central North
blue marlin
von Bertalanffy growth curves..... 553
Scopelengys clarkei, description of new species 142
striped marlin
von Bertalanffy growth curves..... 553

Pacific, eastern
whale, melon-headed
first record in, with summary of world distribution 457
yellowfin tuna
energetics model for an exploited population..... 36

Pacific, eastern tropical
porpoise, spotted
growth and reproduction..... 229

Pacific, North
albacore
tag shedding, estimates of rates 675

Pacific, northeast
halibut, Pacific
mercury content 783
sablefish
mercury content 791

Pagrus pagrus–see Porgy, red

Pandalus hypsinotus–Shrimp, coonstripe

Pandalus jordani
sampler, epibenthic, used to study ontogeny of vertical migration 994

"Paralytic shellfish poisoning in Tenakee, southeastern Alaska: A possible cause," by Steven T. Zimmerman and Robert S. McMahon 679

Parophrys vetulus–see Sole, English

PARRACK, M. L., "Estimation of fishing effort in the western North Atlantic from aerial search data" 503

PEARCY, WILLIAM G., "Seasonal and inshore-offshore variations in the standing stocks of micronekton and macrozooplankton off Oregon." 70

_____–see KEENE and PEARCY

_____–see ROTHLISBERG and PEARCY

PELLA, JEROME J.–see BAILEY et al.

Penaeus aztecus–see Shrimp, brown

Penaeus aztecus subtilis
phosphoglucomutase polymorphism in 453

Penaeus brasiliensis
phosphoglucomutase polymorphism in 453

Penaeus duorarum–see Shrimp, pink

Penaeus setiferus–see Shrimp, white

Peponocephala electra–see Whale, melon-headed

PERRIN, WILLIAM F., "First record of the melon-headed whale, *Peponocephala electra*, in the eastern Pacific, with a summary of world distribution" 457

_____, JAMES M. COE, and JAMES R. ZWEIFEL, "Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific" 229

Petalidium suspiriosum
ecology of Hawaiian 824

"Phosphoglucomutase polymorphism in two penaeid shrimps, *Penaeus brasiliensis* and *Penaeus aztecus subtilis*," by Lawrence M. Lansford, Charles W. Caillouet, and Kenneth T. Marvin 453

Pinfish
feeding ecology, observations of postlarval
current speed and feeding intensity 424
daily rations 425
evacuation rates 424
feeding periodicity 425
food preferences, size related 428
midday feeding, temporal variation 424

Placopecten magellanicus–see Scallop, sea

Plankton, net
Monterey Bay, California
contribution to standing stocks and primary productivity during upwelling season 183

Polychaete variation
application of systematic sampling to study of, in soft substrate environment 942

"Population biology of *Euphausia pacifica* off southern California," by Edward Brinton 733

"Populations of sympatric sculpins, *Cottus aleuticus* and *Cottus asper*, in four adjacent salmon-producing coastal streams on Vancouver Island, B.C.," by J. C. Mason and S. Machidori 131

Porgy, red
North Carolina
fecundity 775
reproductive cycle 775
sex ratios 775

Porpoise, spotted
growth and reproduction in eastern tropical Pacific
color pattern 242
gestation period 234
growth, fetal 234
growth, postnatal 236
Japanese population, comparison with 266
length at birth 234
length-weight relationships 242
production, gross annual 265
reproduction, female 248
reproduction, male 243
reproduction, seasonality 243
schooling in relation to reproduction 265
sex ratios 264

Porpoises
underwater paint marking 287

"Predator-prey relationship between Pacific herring, *Clupea harengus pallasi*, larvae and a predatory hyperiid amphipod, *Hyperoche medusarum*," by Hein von Westernhagen and Harold Rosenthal 669

"Prehatch and posthatch growth of fishes–a general model," by James R. Zweifel and Reuben Lasker 609

"Present and historical spawning grounds and nurseries of American shad, *Alosa sapidissima*, in the Delaware River," by Mark E. Chittenden, Jr. 343

PRISTAS, PAUL J.–see MAY et al.

_____, ELDON J. LEVI, and ROBERT L. DRYFOOS, "Analysis of returns of tagged Gulf menhaden" 112

PROCHASKA, FRED J.–see ALVAREZ et al.

PROCTOR, RAPHAEL–see TRENT et al.

"Production of fry and adults of the 1972 brood of pink salmon, *Oncorhynchus gorbuscha*, from gravel incubators and natural spawning at Auke Creek, Alaska," by Jack E. Bailey, Jerome J. Pella, and Sidney G. Taylor 961

"Production of juvenile chinook salmon, *Oncorhynchus tshawytscha*, in a heated model stream," by Peter A. Bisson and Gerald E. Davis. 763

"Protein taxonomy of the Gulf of Mexico and Atlantic Ocean seatrouts, genus *Cynoscion*," by Michael P. Weinstein and Ralph W. Yerger 599

Pseudopleuronectes americanus–see Flounder, winter

Puget Sound, Washington
  marine fouling
    subtidal and intertidal, on artificial substrata 377
  Pacific salmon
    isolation and description of two vibrios pathogenic to 447

PULLEN, EDWARD J.–see TRENT et al.

Queenfish
  seasonal spawning cycle 983

RALSTON, STEPHEN, "Age determination of a tropical reef butterflyfish utilizing daily growth rings of otoliths" 990

RAVESI, E. M.–see GADBOIS et al.

"Reevaluation of fishing effort and apparent abundance in the Hawaiian fishery for skipjack tuna, *Katsuwonus pelamis*, 1948-70," by Richard N. Uchida 59

"Relation of fish catches in gill nets to frontal periods," by Nelson May, Lee Trent, and Paul J. Pristas 449

"Reproductive cycle, fecundity, and sex ratios of the red porgy, *Pagrus pagrus* (Pisces: Sparidae), in North Carolina," by Charles S. Manooch III 775

"Review of the deep-sea fish genus *Scopelengys* (Neoscopelidae) with a description of a new species, *Scopelengys clarkei*, from the central Pacific," by John L. Butler and Elbert H. Ahlstrom 142

ROGERS, CAROLYN A., "Effects of temperature and salinity on the survival of winter flounder embryos" ... 52

ROSENTHAL, HARALD–see WESTERNHAGEN and ROSENTHAL

ROTHLISBERG, PETER C., and WILLIAM G. PEARCY, "An epibenthic sampler used to study the ontogeny of vertical migration of *Pandalus jordani* (Decapoda, Caridea)" 994

ROTHSCHILD, BRIAN J.–see LORD et al.

Sablefish
  mercury in, from northeast Pacific
    age 795
    geographical location 792
    sex 796
    size 793
    utilization 796

Sagittae
  in nehu, daily growth increments
    age and growth 9

Sahara, Spanish
  pelagic fish eggs and larvae
    distribution and ecology in an upwelling area off .. 885

St. Andrew Bay, Florida
  penaeid shrimp, distribution, abundance, and size ... 158

SAKAGAWA, GARY T., and MAKOTO KIMURA, "Growth of laboratory-reared northern anchovy, *Engraulic mordax*, from southern California" 271

Salinity
  survival, effects on
    winter flounder embryos 52

Salmon
  migrating, high-seas assessment of
    acoustic buoy 104
    receiver-decoder system 104

Salmon, chinook
  production of juvenile in a heated model stream
    associated flora 765
    benthos and drift 765
    disease 769
    food availability 769
    periphyton biomass and sedimentation 771
    physical characteristics of stream 763
    temperature, direct effects on growtn 768
    temperature regulation 764
    temporal changes in production 767

Salmon, coho
  fry, some features of emerging from simulated redds and concurrent changes in photobehavior 167
  life history in Sashin Creek, Alaska
    age determination 904
    escapement size 899
    fecundity 905
    fry, emigration and salinity tolerance 908
    fry and smolts, numbers 907
    growth and age characteristics 911
    interspecific competition 903
    juveniles, age of in stream 910
    juveniles, entering estuary 907
    juveniles, survival of 914
    redd life 902
    retained eggs 905
    spawners, distribution and density 903
    survival and instantaneous mortality rates 917
    survival from potential egg deposition to emergence 913

Salmon, Pacific
  Puget Sound, Washington
    isolation and description of two vibrios pathogenic to 447

Salmon, pink
  production of fry and adults from gravel incubators and natural spawning in Alaska
    adults, recovery of marked 965
    adults, size of returning 968
    adults, timing of return 969
    egg collection and eyeing 962

fry counting and processing 963
fry size and developmental index 967
natural spawning 962
oxygen levels 963
raising eyed eggs to fry stage 962
survival from egg to fry 966
survival from egg to returning adult 967
survival from fry to returning adult 966
survival from marking effects 967
time of emergence and seaward migration 968
water filter and purifier 962
water temperatures 963

Salmon, sockeye
Bristol Bay, Alaska, 1966-67
foods of juvenile in inshore coastal waters 458
Great Central Lake, Vancouver Island
competition for food with the threespine stickleback 647

Salmon, fishery
decision theory applied to simulated data acquisition and management 837

Salmon roe
Japanese
N-nitrosamines, occurrence of volatile 683

Sampling, stratified systematic
infauna variation in soft substrate environment
bivalves 944
polychaetes 942
procedures, field 939
procedures, statistical 939
sediment 941

Santa Barbara, California
reef fishes
day versus night activity in a kelp forest 703

Santa Catalina Island
trophic interactions among fishes and zooplankters .. 567

SANCHEZ, CAROL–see HUNTER and SANCHEZ

Sandab, Pacific
Oregon, continental shelf
food of 984

Sardine, Pacific
California Current
larvae, food and feeding 517

Sardinops sagax–see Sardine, Pacific

Sashin Creek, Alaska
salmon, coho
life history 897

Scallop, sea
life history, ecology, and behavior of *Liparis inquilinus* associated with 409

SCHERBA, STEPHEN, JR., and VINCENT F. GALLUCCI, "The application of systematic sampling to a study of infauna variation in a soft substrate environment" 937

SCHEVILL, WILLIAM E.–see WATKINS and SCHEVILL

SCHIEWE, MICHAEL H.–see HARRELL et al.

Sciaenops ocellata–see Drum, red

Scopelengys
review of genus and description of a new species from central North Pacific 142

Scopelengys clarkei
new species from the cental North Pacific 142

Sculpins
populations of sympatric on Vancouver Island
age determination 133
age structure 136
annual growth, mortality, and length-weight relations 138
biomass distribution 137
distribution and relative abundance 133
general life history 133
population estimates 132
population sampling 132

Sea raven
early development, notes on 467

Searobins
biology of five species from northeastern Gulf of Mexico
bottom type 100
capture, time of 100
depth distribution 99
food habits 102
geographic distribution 99
sexual maturity 101
size-depth relationship 100
spawning season 101
water temperature 100

"Seasonal and inshore-offshore variations in the standing stocks of micronekton and macrozooplankton off Oregon," by William G. Pearcy 70

"Seasonal spawning cycles of the sciaenid fishes *Genyonemus lineatus* and *Seriphus politus*," by Stephen R. Goldberg 983

Seatrouts
protein taxonomy
Atlantic Ocean 599
Gulf of Mexico 599

"Second record of black skipjack, *Euthynnus lineatus*, from the Hawaiian Islands," by Walter M. Matsumoto .. 207

Sergestes armatus
ecology of Hawaiian 810

Sergestes atlanticus
ecology of Hawaiian 805

Sergestes consobrinus
ecology of Hawaiian 813

Sergestes cornutus
ecology of Hawaiian 808

Sergestes erectus
ecology of Hawaiian 809

Sergestes orientalis
ecology of Hawaiian 811

Sergestes pectinatus
ecology of Hawaiian 815

Sergestes sargassi
ecology of Hawaiian 813

Sergestes tanillus
ecology of Hawaiian 812

Sergestes vigilax
ecology of Hawaiian 811

Sergia bigemmea
ecology of Hawaiian 819

Sergia bisulcata
ecology of Hawaiian 822

Sergia fulgens
ecology of Hawaiian 816

Sergia gardineri
ecology of Hawaiian 818

Sergia inequalis
ecology of Hawaiian 821

Sergia laminata
ecology of Hawaiian 824

Sergia maxima
ecology of Hawaiian 823

Sergia scintillans
ecology of Hawaiian 817

Sergia tenuiremis
ecology of Hawaiian 823

Seriphus politus—see Queenfish

Shad, American
spawning grounds and nurseries, Delaware River
adults, areas contributing to successful production of 349
behavior, spawning period 345
spawning period 344
weight loss, mortality, feeding, and duration of residence in fresh water
feeding behavior 153
gonad weight-length relationships prior to spawning 152
somatic weight-length relationships prior to spawning 152
total and fork length conversion 152
total weight-length relationships prior to spawning 152
upstream mortality 153

Shark, bigeye thresher
western North Atlantic, observations on 221

SHARP, GARY D., and ROBERT C. FRANCIS, "An energetics model for the exploited yellowfin tuna, *Thunnus albacares*, population in the eastern Pacific Ocean". 36

Shellfish poisoning, paralytic
Tenakee, southeastern Alaska
possible cause 679

SHERIDAN, PETER F.—see LIVINGSTON et al.

Shrimp
Pandalus jordani
sampler, epibenthic, used to study ontogeny of vertical migration 994

Shrimp, brown
West Bay, Texas
abundance in natural and altered marshes 195

Shrimp, coonstripe
zoeae
description of, reared in laboratory 323

Shrimp, grass
West Bay, Texas
abundance in natural and altered marshes 195

Shrimp, penaeid
St. Andrew Bay system, Florida, distribution, abundance, and size 158

Shrimp, pink
West Bay, Texas
abundance in natural and altered marshes 195

Shrimp, white
West Bay, Texas
abundance in natural and altered marshes 195

Shrimp fleet
Gulf of Mexico
economic and financial analysis of increasing costs. 302

Shrimp processing
dual structural equilibrium in Florida industry
characteristics 881
entry and exit patterns, 1959-71 880
forecasting firm distribution and predicting structural equilibrium 882

Shrimps
ecology of Hawaiian sergestid
color pattern and daytime vertical distribution: role of countershading 825
contamination problem in analysis of vertical distribution data 803
feeding chronology and diet 829
feeding study 803
interspecific relations 831
nighttime vertical distribution and migration 827
Petalidium suspiriosum 824
reproduction and growth 831
sampling area 799
Sergestes armatus 810
Sergestes atlanticus 805
Sergestes consorbrinus 813
Sergestes cornutus 808
Sergestes erectus 809
Sergestes orientalis 811
Sergestes pectinatus 815
Sergestes sargassi 813
Sergestes tantillus 812
Sergestes vigilax 811
Sergia bigemmea 819
Sergia bisulcata 822
Sergia fulgens 816
Sergia gardineri 818
Sergia inequalis 821

Sergia laminata 824
Sergia maxima 823
Sergia scintillans 817
Sergia tenuiremis 823
vertical distribution 800

Silverside, Atlantic
embryos, optical malformations induced by insecticides 208

"Size composition and growth of young rock crab, *Cancer irroratus*, on a rocky beach in Maine," by Jay S. Krouse 949

SKILLMAN, ROBERT A., and MARIAN Y. Y. YONG, "Von Bertalanffy growth curves for striped marlin, *Tetrapturus audax*, and blue marlin, *Makaira nigricans*, in the central North Pacific Ocean" 553

Skipjack, black
Hawaiian Islands, second record 207

SMITH, PAUL E.–see HEWITT et al.

Sole, English
Oregon, continental shelf
food of 984

Sole, petrale
Oregon, continental shelf
food of 984

Sole, rex
Oregon, continental shelf
food of 984

Sole, rock
Oregon, continental shelf
food of 984

"Some features of coho salmon, *Oncorhynchus kisutch*, fry emerging from simulated redds and concurrent changes in photobehavior," by J. C. Mason 167

Sonar mapping
development and use for pelagic stock assessment in California current area
automated hydrocoustic data acquisition and processing system 292
automated sonar survey 294
bottom topography 289
diurnal and seasonal effects 285
experiment, charter boat 291
experiment, fish trap 290
target size 283
target strength 285

Spot
feeding ecology, observations of postlarval
current speed and feeding intensity 424
daily ratios 425
evacuation rates 424
feeding periodicity 425
size related food preferences 428
temporal variation in midday feeding 424

Squid
laboratory-reared
feeding behavior, food consumption, growth, and respiration 176

STADELMAN, DONALD–see TILLMAN and STADELMAN

STAEGER, WILLIAM H., and HOWARD F. HORTON, "Fertilization method quantifying gamete concentrations and maximizing larvae production in *Crassostrea gigas*" 698

Stenella attenuata–see Porpoise, spotted

Stickleback, threespine
Great Central Lake, Vancouver Island
competition for food with juvenile sockeye salmon . 647
distribution, food, and feeding 647

STILLWELL, CHARLES E., and JOHN G. CASEY, "Observations on the bigeye thresher shark, *Alopias superciliosus*, in the western North Atlantic" 221

Stolephorus purpureus–see Nehu

STRUHSAKER, JEANNETTE W.–see KORN et al.

STRUHSAKER, PAUL, and JAMES H. UCHIYAMA, "Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae" 9

Stylocheiron sp.
California Current, central region
density, vertical range, and diel movement 932

"Subtidal and intertidal marine fouling on artificial substrata in northern Puget Sound, Washington," by Charles H. Hanson and Jonathan Bell 377

Swim bladder
anchovy, northern
diel changes in inflation 847

Swimming speed
minimum
tuna, albacore 955

TAYLOR, SIDNEY G.–see BAILEY et al.

TEENY, FUAD M.–see HALL et al.

Temperature
effects on survival
winter flounder embryos 52

Tenakee, Alaska
shellfish poisoning, paralytic
possible cause 679

TENNY, RICHARD D.–see COLLINS and TENNY

Tessarabrachion sp.
California Current, central region
density, vertical range, and diel movement 929

Tetrapturus audax–see Marlin, striped

"Thermal tolerance and resistance of the northern anchovy, *Engraulis mordax*," by Gary D. Brewer 433

Thunnus alalunga–see Tuna, albacore

Thunnus albacares–see Tuna, yellowfin

Thysanoessa sp.
California Current, central region
density, vertical range, and diel movement..... 929

Thysanopoda sp.
California Current, central region
density, vertical range, and diel movement..... 929

TILLMAN, MICHAEL F., and DONALD STADELMAN, "Development and example application of a simulation model of the northern anchovy fishery"..... 118

Totoaba
commercial fishery and reproductive biology in northern Gulf of California
breeding migration..... 534
decline of fishery..... 538
diet..... 537
distribution..... 537
habitat..... 537
history of fishery..... 532
spawning concentration 535

Trachurus symmetricus–see Mackerel, jack

Transmitter, ultrasonic
harness for attachment of
red drum 998

TRENT, LEE–see MAY et al.

_____, EDWARD J. PULLEN, and RAPHAEL PROCTOR, "Abundance of macrocrustaceans in a natural marsh and a marsh altered by dredging, bulkheading, and filling" 195

"Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California," by Edmund S. Hobson and James R. Chess..... 567

Tuna, albacore
Pacific, North
tag shedding, estimates of rates 675
swimming speed, minimum
comparison among four scombrids 958
density variations..... 956
determining 957
estimates, field..... 959
west coast
troll fishermen, comparison of the most successful and least successful..... 973

Tuna, skipjack
reevaluation of fishing effort and apparent abundance in Hawaiian fishery, 1948-70
catch reports..... 60
comparison of catch per effective trip and catch per day fished 62
differences in catch per effective trip between vessel classes, between areas, and among years..... 64
fishing areas..... 61
interrelation of total catch, fishing intensity, and apparent abundance..... 67
measures of apparent abundance and fishing intensity..... 66
relation between catch per day fished and catch per effective trip..... 64
reporting of zero-catch trips..... 60
sources of variability in fishing power among vessels 60
standardization of catch per day fished 66
vessels, classes of..... 61

Tuna, yellowfin
energetics model for an exploited population
food as a population regulator 46
population dynamics..... 37
spawning survival versus population biomass 47
total drag determination..... 41
velocity determination..... 41

Turkey
fed tuna oil with and without α-tocopherol supplement or injection
effects of cooking in air or nitrogen on development of fishy flavor in breast meat 89

Uca pugilator–see Crab, fiddler

UCHIDA, RICHARD N., "Reevaluation of fishing effort and apparent abundance in the Hawaiian fishery for skipjack tuna, *Katsuwonus pelamis*, 1948-70" 59

UCHIYAMA, JAMES H.–see STRUHSAKER and UCHIYAMA

"Underwater paint marking of porpoises," by William A. Watkins and William E. Schevill..... 687

United States
continental shelf and slope, eastern coast
Ceriantharia, Zoanthidea, Corallimorpharia, and Actiniaria..... 857

"Uptake, distribution, and depuration of ^{14}C-benzene in northern anchovy, *Engraulis mordax*, and striped bass, *Morone saxatilis*," by Sid Korn, Nina Hirsch, and Jeannette W. Struhsaker..... 545

Vancouver Island, British Columbia
Cottus aleuticus and *Cottus asper*
populations of sympatric in four adjacent salmon-producing coastal streams..... 131

"Vertical distribution and diel migration of euphausiids in the central region of the California Current," by Marsh J. Youngbluth..... 925

"Vertical distribution and other aspects of the ecology of certain mesopelagic fishes taken near Hawaii," by Thomas A. Clarke and Patricia J. Wagner 635

Vibrios
Puget Sound, Washington
isolation and description of two, pathogenic to Pacific salmon 447

"Von Bertalanffy growth curves for striped marlin, *Tetrapturus audax*, and blue marlin, *Makaira nigricans*, in the central North Pacific Ocean," by Robert A. Skillman and Marian Y. Y. Yong..... 553

WAGNER, PATRICIA J.–see CLARKE and WAGNER

WALTERS, JOHN F., "Ecology of Hawaiian sergestid shrimps (Penaeidea: Sergestidae)"..... 799

WARDLAW, NEWTON J.–see GRIFFIN et al.

WATKINS, WILLIAM A., and WILLIAM E. SCHEVILL, "Underwater paint marking of porpoises" 687

Weakfish
reproductive biology in North Carolina 18

"Weight loss, mortality, feeding, and duration of residence of adult American shad, *Alosa sapidissima*, in fresh water," by Mark E. Chittenden, Jr. 151

WEINSTEIN, MICHAEL P., and RALPH W. YERGER, "Protein taxonomy of the Gulf of Mexico and Atlantic Ocean seatrouts, genus *Cynoscion*" 599

WEIS, JUDITH S., "Effects of mercury, cadmium, and lead salts on regeneration and ecdysis in the fiddler crab, *Uca pugilator*" 464

_____, and PEDDRICK WEIS, "Optical malformations induced by insecticides in embryos of the Atlantic silverside, *Menidia menidia*" 208

WEIS, PEDDRICK–see WEIS and WEIS

West Bay, Texas
macrocrustaceans, abundance in a natural marsh and a marsh altered by dredging, bulkheading, and filling.. 195

WESTERNHAGEN, HEIN VON, and HARALD ROSENTHAL, "Predator-prey relationship between Pacific herring, *Clupea harengus pallasi*, larvae and a predatory hyperiid amphipod, *Hyperoche medusarum*" 669

Whale, melon-headed
Pacific, eastern
first record in, with summary of world distribution 457

WICKHAM, DANIEL E.–see FISHER and WICKHAM

WIDERSTEN, BERNT, "Ceriantharia, Zoanthidea, Corallimorpharia, and Actiniaria from the continental shelf and slope off the eastern coast of the United States" 857

YERGER, RALPH W.–see LEWIS and YERGER

_____–see WEINSTEIN and YERGER

YONG, MARIAN Y. Y.–see SKILLMAN and YONG

YOUNGBLUTH, MARSH J., "Vertical distribution and diel migration of euphausiids in the central region of the California Current" 925

ZIMMERMAN, STEVEN T., and ROBERT S. McMAHON, "Paralytic shellfish poisoning in Tenakee, southeastern Alaska: A possible cause" 679

Zoanthidea
continental shelf and slope, U.S. east coast
Epizoanthus incrustatus 858

Zooplankers
Santa Catalina Island
trophic interactions with fishes 567

Zooplankton
California Current, central region
density, vertical range, and diel movement..... 925

ZWEIFEL, JAMES R.–see PERRIN et al.

_____, and REUBEN LASKER, "Prehatch and posthatch growth of fishes–a general model"..... 609

ERRATA

Fishery Bulletin, Vol. 74, No. 3

Skillman, Robert A., and Marian Y. Y. Yong, "Von Bertalanffy growth curves for striped marlin, *Tetrapturus audax*, and blue marlin, *Makaira nigricans*, in the central North Pacific Ocean," p. 553-566.

1) Page 563, left column, line 8, correct line to read:
all 11 age-groups for females and using 12 and 11 (deleting oldest)

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Contents—continued

SCHERBA, STEPHEN, JR., and VINCENT F. GALLUCCI. The application of systematic sampling to a study of infauna variation in a soft substrate environment 937
KROUSE, JAY S. Size composition and growth of young rock crab, *Cancer irroratus*, on a rocky beach in Maine 949
DOTSON, RONALD C. Minimum swimming speed of albacore, *Thunnus alalunga* .. 955
BAILEY, JACK E., JEROME J. PELLA, and SIDNEY G. TAYLOR. Production of fry and adults of the 1972 brood of pink salmon, *Oncorhynchus gorbuscha*, from gravel incubators and natural spawaning at Auke Creek, Alaska 961
KEENE, DONALD F., and WILLIAM G. PEARCY. Comparison of the most successful and least successful west coast albacore troll fishermen 973

Notes

GOLDBERG, STEPHEN R. Seasonal spawning cycles of the sciaenid fishes *Genyonemus lineatus* and *Seriphus politus* 983
KRAVITZ, MICHAEL J., WILLIAM G. PEARCY, and M. P. GUIN. Food of five species of cooccurring flatfishes on Oregon's continental shelf 984
RALSTON, STEPHEN. Age determination of a tropical reef butterflyfish utilizing daily growth rings of otoliths 990
ROTHLISBERG, PETER C., and WILLIAM G. PEARCY. An epibenthic sampler used to study the ontogeny of vertical migration of *Pandalus jordani* (Decapoda, Caridea) 994
CARR, WILLIAM E. S., and THOMAS B. CHANEY. Harness for attachment of an ultrasonic transmitter to the red drum, *Sciaenops ocellata* 998

INDEX, VOLUME 74 1001

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